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BIOLOGICAL BULLETIN

STUDIES ON THE RELATION BETWEEN AMITOSIS AND MITOSIS

II. Development of the Testes and Spermatogenesis in Moniezia (*Continued*).

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IV. *The Spermatocytic Mitoses.*

The appearance of the chromosomes of the first maturation division follows the stage shown in Fig. 13, *A* (Pl. X.). Figs. 14, *A*, 14, *B*, and 15 (Pl. XI.) show this stage in *M. expansa*, Figs. 16, *A*–16, *C* (Pl. XI.), in *M. planissima*. In the former species eight of these chromosomes have been counted in the nuclei in some twenty-five cases (Fig. 14, *A*) and in no case have more than eight been found. In many cases, however, it has been impossible even with the utmost care in examining successive sections, to find eight, only seven or six (Fig. 14, *B*) being visible. As regards the number in *M. planissima* the results are less definite. In some cases eight (one of the nuclei in Fig. 16, *C*) in others nine (the other nucleus in Fig. 16, *C*) have been counted and in one (Fig. 16, *B*) case thirteen distinct masses of chromatin were visible in one nucleus. This, however, was probably an earlier stage for some of these masses appear to be grouped in pairs. Fig. 16, *A*, shows two nuclei of *M. planissima* in which five of these chromosomes are visible. It was impossible to determine whether parts of these nuclei were in the next section. One reason for the greater uncertainty in regard to *M. planissima* lies in the fact that these stages were much less frequently seen in my sections of this species than in those of *M. expansa*. I believe that the utmost caution should be used in observations of

this kind. In a study of cytological literature it is difficult to resist the impression that some of the apparent uniformity in cytological phenomena which appears so remarkable and mysterious is in reality the result of the selection of certain "typical" cases and the discarding of others. While I should not venture to assert positively that the number of chromosomes in either of these species of *Moniezia* is actually variable, this certainly appears to be the case, and the evidence given in support of the conclusion that the number of chromosomes in a given species or variety is invariable has not always carried conviction to my mind.

However, the description of the spermatocytic divisons is not the chief object of the present paper and although I have spent much time in endeavoring to reach well-founded conclusions in regard to the number of chromosomes in *Moniezia* it has not been possible for *M. planissima*. In *M. expansa*, as noted above, the maximal number counted during maturation was eight.

In some of the nuclei at this stage these chromosomes appear, as in many other forms in a more or less regular grouping about the periphery of the nucleus. The figures do not show this condition particularly well but Figs. 14, *A*, 14, *B*, 16, *A*, 16, *C* (Pl. XI.), were drawn from nuclei in which the chromosomes were thus arranged. Such nuclei are recognizable at once in a section. This condition, however, was not very commonly found; much more frequent was the condition shown in Fig. 15 where they were irregularly disposed, some at the periphery, others near the center. It is possible that the stage of peripheral arrangement is of relatively short duration and is therefore less frequently seen, but there is also a possibility that it is not of universal occurrence. The question may be left open for the present.

In Fig. 17 (Pl. XI.) two of these chromosomes are shown, both from nuclei with membranes still intact. At the stage figured the fusion of the two parts is not yet complete. So far as actual observation goes these chromosomes of the first maturation division are dyads, not tetrads, no indication of quadrivalence having been observed at any stage, and although they correspond as regards ultimate fate with the tetrads of various authors, I prefer to designate them as what they appear to be — dyads. In consequence of their small size, almost spherical form in late stages,

and close approximation in the spindle no data regarding the direction of the two divisions could be obtained.

As stated in the preceding section the spermatocytes often appear in groups, the pear-shaped members of which are connected at the pointed end by strands of cytoplasm. As the first spindle forms the fusion of the cells proceeds (Fig. 18, Pl. XI.) until in many cases the metaphases of a number of nuclei lie in a continuous mass of cytoplasm, the cytophore (Fig. 19, Pl. XI.). Often, however, the central region of the mass consists for a considerable time of a large space traversed by strands of cytoplasm (Figs. 18, 20, 23 (Pl. XI.), 25 (Pl. XII.). The strands of cytoplasm are represented in a somewhat diagrammatic manner.) In other cases the first spermatocytes are entirely isolated (Fig. 21, Pl. 11).

The spindle appears to be formed largely from the nuclear substance. The fibers are very delicate and no asters are visible (Figs. 18 and 19, Pl. XI.). At the poles are very minute, but fairly distinct deeply-staining, centrosomes. In the masses resulting from the fusion of several spermatocytes the spindles are, so far as observed, always tangential or nearly so (Figs. 19 and 20, Pl. XI.). Just before their division the dyads assume the form seen in Fig. 22 (Pl. XI.), where one is viewed from the side, the other from the surface. Fig. 20 (Pl. XI.) shows the anaphase. Division of the centrosomes has not been observed, as they cannot be distinguished after the chromosomes have approached the poles. Fig. 23 (Pl. XI.) shows the telophase of the first spermatocytic division in a group. The cytoplasm of the cells which formed the group now constitutes a cytophore in which the masses of chromatin lie. It is less dense in appearance and stains less deeply than in earlier stages, where it was concentrated about particular nuclei. The chromatin masses remain at the periphery and the central region is often still more or less vacuolated. Where isolated spermatocytes divide the result is the same: no division of the cytoplasm follows nuclear division, and a cytophore differing from the group-cytophore merely as regards size is formed.

The second division follows the first, in most cases apparently without the formation of a "resting nucleus" between the two. In a few cases, however, nuclei larger than spermatid nuclei and

containing irregular strands and masses of chromatin as if in preparation for a division were formed about the periphery of a cytophore (Fig. 24, Pl. XI.). These were very probably stages following the first spermatocytic division.

Fig. 25 (Pl. XII.) shows the metaphase of the second spermatocytic division in a group cytophore. Here again the divisions are more or less nearly tangential. Fig. 26 (Pl. XII.) shows the anaphase in a portion of a group.

V. *The Fragmentation of Spermatocyte Nuclei.*

In Section III. (pp. 181–182) it was stated that certain of the nuclei of the first spermatocytes become larger than the others, and that the spireme instead of becoming more dense and giving rise to chromosomes becomes less dense and very irregular and the nucleolus remains instead of disappearing (Fig. 13, *B*, Pl. X.). These nuclei constitute the earliest recognizable stage in a remarkable process of fragmentation which is apparently a normal phenomenon in the testes of both species of *Moniezia*. The process is so entirely different from anything described in the spermatogenesis of other forms that at first I regarded it as a form of degeneration. But repeated examination of old and new material during four successive years has convinced me that the process gives rise to nuclei which are indistinguishable from the spermatid nuclei which have arisen by mitosis. Whether these "spermatid nuclei" resulting from the fragmentation of spermatocyte nuclei actually take part in the formation of functional spermatozoa it is impossible to determine, but that spermatozoa structurally similar to those developing from nuclei which arise in the ordinary manner develop from these spermatids is, as will appear probable.

This process, like the typical spermatogenesis, occurs in isolated cells or simultaneously in groups. In the latter case the different members of the group fuse together, in the manner described in the preceding section, and this cytoplasm forms a cytophore. It is rare, however, that groups so regular in form and arrangement as that shown in Fig. 27, *A* (Pl. XII.), are found More commonly only two or three cells fuse together or the process occurs in isolated cells. Fig. 27, *A* (Pl. XII.) shows a

group of the nuclei in most of which the spireme is apparently breaking up and disappearing. It stains less deeply than in earlier stages and appears to be separating into irregular masses. Fig. 27, *B* (Pl. XII.), shows an exceptionally clear case, in which some portions of the spireme are apparently breaking up into granules. Figs. 27, *C*, and 27, *D* (Pl. XII.), show still other cases. It will be observed that the nucleolus retains its staining power: as a matter of fact it undergoes no visible change.

Except for the spireme or its remnants the nucleus shows with the usual degree of extraction no visible structural features. As it increases in size the nuclear membrane becomes increasingly difficult to distinguish and finally disappears, so that what was formerly the nucleus appears merely as a cavity in the cytoplasm containing the nucleolus and irregular shreds and granules of chromatic substance usually situated at one side (Figs. 27, *B*, 27, *C*, 27, *D*, 28, Pl. XII.). The whole appears as if degenerating. In these and the following figures the boundaries of the nuclear cavities and the spaces in the cytoplasm which remain in the later stages are indicated by broken lines.

But the observations now to be described afford very strong evidence in favor of the view that these nuclei do not undergo complete degeneration. In and about these cavities containing the remains of the spireme and the nucleolus very small new nuclei with one or a few small granules of chromatin appear to be formed. In Fig. 28 (Pl. XII.), one such nucleus is shown in one of the cells: in Figs. 29, *A*, and 29, *B* (Pl. XII.), two appear in each cell: in Fig. 29, *C* (Pl. XII.), is one a little larger than the preceding; in this case the fragmenting nucleus lies in a cytophore with spermatids already formed and from one of which a spermatozoön is developing: in Fig. 29, *D* (Pl. XII.), are again two of the small nuclei. The nature of the process appears to be somewhat as follows: as the old nuclear membrane breaks down the cytoplasm encroaches more or less upon the nuclear cavity and a new membrane forms about some of the particles or masses of chromatin. This is not very different from what occurs in various forms when a single chromosome or a few chromosomes are separated from the rest during division.

But the new nuclei are not always so small as these shown in

Figs. 28 and 29, *A*–29, *D*. Figs. 30, *A*–*C* (Pl. XIII.), show cases in which they are somewhat larger, and in which the method of their formation is more clearly visible. In these cases the new nuclei are nearly hemispherical in form and appear as if growing or budding out from the cavity representing the old nucleus into the cytoplasm about it. Whether the method of formation is actually the same in all cases is doubtful; sometimes the new nuclei seem to lie wholly within the cavity as in Figs. 29, *A* and 29, *B* (Pl. XII.). But there can be no doubt of their formation. The newly formed nuclear membrane is quite distinct and the whole process presents a very characteristic appearance.

The number of deeply staining bodies visible within these small nuclei depends on the fixation and staining. If extraction is carried beyond a certain point only one dark body retains the stain: otherwise several may be visible, one or two of which are usually larger than the others. After chrom-oxalic the stain is more readily extracted from all except the one body and with the usual degree of extraction only the one body appears. Figs. 29, *A*–29, *D*, are from such preparations. In nearly all cases the nuclei stain somewhat more deeply throughout than the cytoplasm as is indicated in the figures by stippling.

Whether the number of new nuclei formed is always the same is uncertain but it is probable that as many as three or four and perhaps more new nuclei may arise from one old nucleus. In Fig. 29, *E* (Pl. XII.), four small nuclei lie near the lower nuclear cavity but some of these may have arisen from another nucleus.

Figs. 31–36 (Pl. XIII.), show what I regard as later stages in this process. In the group shown in Fig. 31 two spermatocytes were apparently involved and the two old nuclear cavities are still visible, though very irregular in form and divided by strands of cytoplasm. One of the old nucleoli is visible, the other lying in another section. Judging from their position three of the small nuclei were formed about the cavity on the right and one on the other: in the next section more small nuclei were found which probably belonged to the nuclear cavity on the left but in this section other adjoining nuclear cavities with other small nuclei appeared, so that certainty was impossible. It is of in-

terest to note that some of the nuclei in the figure are distinctly hemispherical as if they had been formed in the manner represented in Figs. 30, *A*–30, *C*.

In Fig. 32 (Pl. XIII.) three cavities appear, the old nucleolus being visible in the one on the right. In the middle cavity there are four nuclei. Fig. 33 (Pl. XIII.) shows another case in which portions of two nuclear cavities are visible, each with its nucleolus, and seven nuclei, four about one cavity, three about the other.

In Figs. 34, 35 and 36 (Pl. XIII.) groups of nuclei are shown lying in cavities of the cytophore: nucleoli were not visible in this section and it was impossible to determine how many spermatocytes were involved in the formation of these groups. That such groups as these are formed by fragmentation there can, I think, be no doubt. In all cases where the spermatocytes divide mitotically in groups the spindles lie peripherally and nearly tangentially in the cytophore (Figs. 19, 20, 23, Pl. XI.; 25, 26, Pl. XII.), and the nuclei formed lie at or near the periphery (Figs. 24, Pl. XI.; 42, 43, 44, Pl. XIV.). There are no grounds for supposing that they migrate from the periphery and return to it; moreover, it is difficult to see how nuclei grouped as those in Figs. 34 and 35 (Pl. XIII.) are grouped could have been formed *in situ* by mitosis. It seems probable that this difference in position is quite sufficient to distinguish the nuclei formed by fragmentation of spermatocytes from those formed by the spermatogenetic mitoses.

Assuming that these nuclei have arisen by the fragmentation of spermatocytes, the number of chromatin granules has increased beyond that contained in some of the nuclei at the time of their formation and the nuclei are now somewhat larger than some of those. No further growth takes place, however. The nuclei themselves are indistinguishable from those spermatid nuclei which lie at the periphery of the cytophores and are doubtless the products of mitoses (Figs. 42, 43, Pl. XIV.).

Figs. 37 (Pl. XIII.) and 38 (Pl. XIV.) represent larger areas of two testes showing how the nuclei which, judging from their position in the cytophore, have arisen by fragmentation are situated in relation to other stages. No trace of definite position or arrangement of the various stages in the testis could be found.

But these nuclei apparently do not remain massed together in the cytophore. There is every reason to believe that they migrate to the periphery. Very frequently cytophores with several old nucleoli imbedded in different regions of their cytoplasm, indicating that fragmentation has occurred, show all their nuclei at the periphery as in the case of spermatids formed by mitosis. Since I have never found first spermatocytic mitoses and fragmentation occurring in the same cytophore and since the nucleolus disappears before mitosis it seems probable that the presence of the old nucleoli which stain very characteristically and are readily recognizable is sufficient to identify a particular cytophore and its spermatid nuclei, for such, I believe we may call them, at least so far as appearance goes, as the result of fragmentation.

Fig. 39 (Pl. XIV.) is probably a stage in the migration to the periphery of spermatid nuclei formed by fragmentation. At the right of the figure one of the old nucleoli, itself near the periphery, and a part of an old nuclear cavity containing a few granules are visible: another lies near the middle of the cytophore and still others were found in the same cytophore in other sections. Some of the nuclei have already reached the periphery of the cytophore and the cytoplasm about them bulges from its surface. Most of these nuclei are more or less hemispherical with convex surface toward the periphery and a space adjoins the flattened side: this condition is probably connected with the migration of the nuclei toward the periphery. Indeed, it is not impossible that this migration may not be a bodily movement through the cytoplasm of the cytophore, but rather the continued formation of new nuclear membrane on the peripheral side and its continued disappearance on the proximal side. In any case the change of position is probably a "tactic" reaction of some sort.

In two testes cytophores have been found containing nuclei intermediate in size between those of the spermatocytes at the time of fragmentation and those of spermatids, but which appeared as if preparing for fragmentation. Fig. 40 shows one of these cases. These two groups may possibly be cases of secondary fragmentation. Occasionally as in Fig. 30, *A* (Pl. XIII.), the nuclei arising by fragmentation are unusually large and perhaps

undergo fragmentation again. At any rate such cases are rare and not of fundamental importance. In one case a mitotic spindle was observed in a cytophore whose nuclei had apparently arisen by fragmentation since two nucleoli were present and the nuclei were not at the periphery (Fig. 41, Pl. XIV.). This would appear to be a case where a nucleus resulting from fragmentation divides mitotically afterward: it might, however, be a case where a spermatocyte undergoing mitosis had fused with a group undergoing fragmentation: if that were the case the size of the spindle would seem to identify it as the second spermatocytic division. But whatever its interpretation, this, too, is clearly an exceptional case. It is probable that a large proportion of the nuclear substance of the spermatocyte passes into the cytoplasm at the time of fragmentation. It may be that a kind of reduction is accomplished in this manner.

The relative frequency of fragmentation and mitosis seems to vary in different chains, proglottids and testes. In some chains the spermatogenetic mitoses were rarely seen except in the older proglottids, yet spermatozoa were produced in the younger proglottids as abundantly apparently as elsewhere. In some other cases mitosis is more frequent. From examination of the testes one gains the impression that the mitoses are not in any case sufficiently numerous to account for the large number of spermatids and spermatozoa formed. I regard it as at least probable that spermatozoa are produced from the "spermatid" nuclei which arise by fragmentation, as well as even those which arise by mitosis. As will appear in a later section, some cells undergo degeneration in almost all or all testes and it is of course impossible to prove that these particular spermatid nuclei which arise by fragmentation do not undergo degeneration. Still, developing spermatozoa have been found on cytophores containing the old spermatocyte nucleoli.

VI. *The Formation of the Spermatozoön from the Spermatid.*

In consequence of the difficulty of observation of details in these exceedingly minute structures, which is farther increased by the massing together of the spermatids in cytophores and the condensation of these in later stages, it has not been possible to reach positive conclusions on all points. It can scarcely be

doubted from my own observations as well as those of others that the development of the spermatozoön in these forms differs in certain respects from the typical method. Although the greatest caution has been observed throughout, the observations are given with a certain reserve, because it was impossible to attain complete certainty on many points and because they are not in accord with commonly accepted opinions regarding the development of the spermatozoön. I believe, however, that a careful investigation of spermatogenesis in the cestodes will prove of interest.

Except in the early stages when the spermatid nuclei produced mitotically appear in pairs about the cytophore (Fig. 42, Pl. XIV.) and those arising by fragmentation of the spermatocytes are massed in the interior of the cytophore (Figs. 34–36, Pl. XIII.) there is no certain criterion for distinguishing the two kinds. The presence of old nucleoli in a cytophore render it probable that all or a part of the spermatid nuclei of that cytophore have arisen by fragmentation, but beyond this no means of identifying the nuclei of different origin has been discovered.

The following account concerns the spermatids without respect to origin. If my conclusions are correct, however, many of these may be the results of fragmentation. As was noted above, developing spermatozoa not different in appearance from others have often been found on cytophores containing the old nucleoli.

Figs. 42 and 43 (Pl. XIV.) show the newly formed spermatid nuclei after mitosis. In Fig. 43, from *M. planissima*, five chromatin granules are distinctly visible in each of the nuclei. These may represent five chromosomes: it is possible that the spermatocytes of this species contained only five dyads (Fig. 16, *A*, Pl. XI.) and that the cases where a larger number seemed to be present (Figs. 16, *B*, 16, *C*, Pl. XI.) were only earlier stages before the chromatin had become massed in the dyads.

After the formation of the spermatid nuclei their peripheral position on the cytophore becomes more and more marked until finally each is borne on a short peduncle or stalk of cytoplasm (Fig. 44, Pl. XIV.). The cytophores differ greatly in size according as they were formed from a single spermatocyte or a larger number: in fact in older testes single isolated spermatids

are sometimes found which have apparently become entirely separated from the cytophore.

The spermatid nuclei contain at this time only a few very distinct deeply staining granules (some of the nuclei in Fig. 44, Pl. XIV.): in cases where extraction is carried to extremes only two granules, one at the peripheral end of the nucleus, the other near the middle or at one side of the nucleus (some of the nuclei in Fig. 44, Pl. XIV.). The peripheral granule is closely applied to the nuclear membrane, so closely indeed that it is often difficult to determine whether it is inside or outside the nucleus. In some cases, however, it is clearly inside the nucleus (Fig. 44, Pl. XIV.) and this is probably its position in all cases.

The first visible step in the formation of the spermatozoön is the appearance at the periphery of the cytoplasm peripheral to the nucleus of a minute deeply staining granule. In position this granule corresponds to the peripheral centrosome which enters the middle piece in the spermatozoa of many other forms. It has been impossible in consequence of the small size of these cells to obtain any data regarding its origin in this case. If the spermatids arising by fragmentation do produce spermatozoa the question as to its origin in those cases is of some interest. This peripheral body which apparently lies in contact with the border of the cytoplasm appears to be connected by a very delicate cytoplasmic strand or fiber with the granule at the peripheral end of the nucleus (Figs. 44 and 45, Pl. XIV.). Whether there is another cytoplasmic granule in contact with or near the nucleus corresponding in position to the other centrosome of other forms could not be determined. From the peripheral granule in the nucleus the delicate fiber appears to continue through the nucleus usually to the second granule (some of the nuclei in Fig. 44, also Fig. 45, Pl. XIV.). This continuation of the fiber within the nucleus has been a matter of the most careful examination and I can say regarding it only that I have seen it in the nuclei of practically every cytophore examined and under the most various conditions of fixation and staining so that if present methods of technique permit trustworthy conclusions in regard to such matters its existence seems beyond doubt. The figures exaggerate its distinctness to some extent. It does not stain as

deeply as the granules themselves but this is very likely due to its smaller diameter.

The next step is the formation of the tail which appears first as a delicate thread extending from the granule at the border of the cytoplasm (Fig. 46, Pl. XIV.).

Figs. 47, *A*–47, *E* (Pl. XIV.) show the developing spermatozoa after different methods of fixation and staining: Fig. 47, *A*, is from *M. expansa* after sublimate and Delafield's hæmatoxylin; Fig. 47, *B*, *M. expansa* after sublimate and iron-hæmatoxylin; Fig. 47, *C*, *M. planissima*, after chrom-oxalic and iron-hæmatoxylin; Fig. 47, *D*, *M. expansa*, after Hermann and iron-hæmatoxylin. Fig. 47, *E*, is from *M. planissima* after sublimate and iron-hæmatoxylin, but with extraction stopped at an earlier stage. One interesting point in this figure as compared with the others is the much larger size of the peripheral cytoplasmic granule and the fiber connecting it with the nucleus — an excellent illustration of the uncertainty attending the use of iron-hæmatoxylin.

The tail of the spermatozoön grows to a very great length. Fresh spermatozoa obtained by teasing living proglottids in indifferent fluids are 0.3–0.4 mm. in length. Most or all the tails arising from one cytophore usually lie parallel in the testis, and since their length is much greater than the diameter of the testis they become coiled in the spaces between the cells or along the wall of the testis. The tail is very delicate and without visible differentiation in structure.

As regards the formation of the head of the spermatozoön *Moniezia* does not seem to agree with other species described. At least I know of no other case in which the sperm-head, if it can be called a head, is formed in the manner described below.

In my study of spermatogenesis I was for a long time puzzled by the fact that all of the sperm nuclei appeared to degenerate after the tails were formed. Masses like Fig. 49 (Pl. XV.) consisting of degenerating nuclei and condensed cytophore cytoplasm can be found in every older testis. At first I concluded that these were probably the spermatids formed by fragmentation which began the development of spermatozoa but were unable to complete it. But another feature made the matter still

more puzzling. The most careful examination, under varied conditions of fixation and staining, of spermatozoa in the male ducts and in the seminal receptacle of the female ducts, which becomes greatly distended with them at a certain stage, failed absolutely to reveal the existence of a head differing in appearance from the tail. The examination and staining of fresh spermatozoa from the seminal receptacle and ducts of living proglottids led to the same result. The spermatozoa appeared as very long thread-like structures perhaps slightly larger at one end than at the other but without the least trace of a physically or chemically differentiated head.

Then the question arose as to whether the eggs were actually fertilized by these spermatozoa. As will be described in the following paper, the spermatozoa were found entering the eggs as these passed the opening from the seminal receptacle on their way to the uterus, and nuclei which could be nothing else than male pronuclei unless these eggs differ from other known cases in their maturation and fertilization stages were found. Returning to the developing spermatozoa the most careful study was made of the various stages and especially of the masses like Fig. 49 (Pl. XV.) which were apparently undergoing degeneration. It is very difficult to distinguish details in these masses for they stain more deeply as they condense and the nuclei especially become more or less filled with deeply staining granules and masses. In the course of time certain apparently favorable cases were found some of which are shown in Figs. 48, *A*–48, *C* (Pl. XV.). These seem to indicate that the "head" of the spermatozoön, *i. e.*, the part arising from the nucleus is formed from the two nuclear granules, the peripheral and the other which may be central or proximal, together with the connecting strand, and furthermore, that when degeneration of the other parts of the nucleus begins the spermatozoön is set free. Figs. 48, *A*–48, *C*, show examples of the early stages of nuclear degeneration in sperm cytophores. In Fig. 48, *C*, the spermatozoön head is apparently in the act of escaping from the degenerating nucleus. The peripheral portion of the nuclear membrane has disappeared but the peripheral nuclear granule is still recognizable. Figs. 48, *A*, and 48, *B*, are apparently somewhat earlier stages in

which the nuclear membrane is still intact. I am forced therefore to the conclusion that only a part of the nucleus is concerned in the formation of the sperm-head, the remainder undergoing degeneration. Fig. 49 (Pl. XV.) represents a cytophore after condensation. For the sake of clearness only a few of the nuclei which cover the surface of the mass are represented as they appear, the others being indicated by dotted lines. In several cases what seems to be the sperm-head is visible in the degenerating nucleus.

Fig. 50 (Pl. XV.) represents a case in which the spermatozoa are apparently just separating from the cytoplasm of the cytophore which contains the deeply staining remains of the nuclei. In this case I convinced myself that these were the anterior ends of the spermatozoa, by following the tails throughout their whole length in the testis. The diameter of the ends shown in the figure was distinctly though only slightly greater than that of the other ends, but the change in diameter is very gradual.

In the free spermatozoa no differentation in staining of the head-region is visible. The whole spermatozoön stains uniformly and less intensely than the nuclear granules or masses of earlier stages. In a few cases I believed I had distinguished slight traces of the two nuclear granules in the fully developed spermatozoön but these observations were so doubtful that no figures are given.

In the fresh spermatozoa obtained by teasing in indifferent fluids no visible head and no movement was ever observed. An examination of the bibliography of the subject afforded scanty results. So far as I have been able to determine no full account of the spermatogenesis of the cestodes exists. Among the older papers several give brief descriptions of the formation of the spermatozoa but these are either very incomplete or incorrect in consequence of the technique employed and need not be reviewed in detail. In one point, however, the early observations agree fairly well: the head of the spermatozoön is described and figured as exceedingly minute or is said to be absent. Sommer and Landois[1] in describing the testes of *Bothriocephalus latus* mention spermatozoa bearing at one end "ein kleines, stark lichtbrechendes Köpfchen."

[1] Sommer and Landois, "Ueber den Bau der geschlechtsreifen Glieder von *Bothriocephalus latus* Bremser," *Zeitschr. f. wiss. Zoöl.*, Bd. XXII., 1872.

Two years later Salensky[1] states that in *Amphilina* the nuclei disappear completely in the formation of the spermatozoa and that "die Kerne bei der Bildung der Spermatozoen keine Rolle spielen." Regarding the fully formed spermatozoa he says: "Die Fäden sind sehr lang, ungefahr 0.27 mm. und an einen Ende etwas gekrummt. Diese Krümmung soll aber nicht als Köpfchen angesehen werden, indem die spermatozoen in ihrer ganzen Länge gleich dick sind."

As regards *Tænia mediocanellata* and *Tænia solium* Sommer[2] speaks of the bundles of spermatozoa which hang from certain large cells (in reality the cytophores) and "mit ihren äusserst feinen, glänzenden Köpfchen noch in Zellenprotoplasma stecken." These "Köpfchen" are probably the nuclear granules which present this appearance in unstained or slightly stained preparations, the nuclear membrane not being clearly visible. "Zwischen diesen Samenfäden producirenden Zellen findet man gleichzeitig im Hodenkörperchen kleine Anhäufungen freier, heller, scharf contourirter und bläschenförmiger Kerne. Einzelne derselben haben an ihrem Grenzrande noch Spuren von Protoplasma in welchen mit seinem glänzenden punctförmigen Köpfchen ein Samenfädchen haftet." These masses are perhaps degenerating cytophores. In another paragraph he describes the formation of the large multinucleate cells which give rise to the spermatozoa and says: "An der Peripherie dieser grossen Zellen geht von irgend einer Stelle die Bildung der Samenfäden aus. Letztere entstehen lediglich aus dem Protoplasma der Zelle; eine Betheiligung der Kerne dabei findet nicht statt. In demselben Maasse wie mit der Bildung der Samenfäden das Protoplasma der Zelle schwindet, werden die eingelagerten Kerne frei, erscheinen dann schärfer berandet wie früher, etwas aufgebläht oder gequollen, homogen und wasserhell, dann fallen sie zusammen, collabiren, wie wenn sie einen flussigen Inhalt entleert hatten und gehen zu grunde, oder werden, wenn sich inzwischen Samengänge ge-

[1] Salensky, "Ueber den Bau und die Entwickelungsgeschichte der *Amphilina*, G. Wagen (*Monostomum foliacium* Reed)," *Zeitschr. f. wiss. Zool.*, Bd. XXIV., 1874.

[2] Sommer, "Ueber den Bau und die Entwickelung der Geschlechtsorgane von *Tænia mediocanellata* (Küchenmeister) und *Tænia solium* (Linné)," *Zeitschr. f. wiss. Zool.*, Bd. XXIV., 1874.

bildet haben mit den Samenfäden fortgespielt." Sommer's preparations were obtained by maceration and teasing and without staining. As described, the fate of the nuclei does not differ very widely from that described in the present paper except for the fact that Sommer failed to observe that any portion of the nucleus took part in the formation of the spermatozoön. Considering the methods employed this failure is not strange.

Moniez[1] describes the formation of large multinucleate cells and the protrusion from their surface of the nuclei which are united with the body of the cell by pedicels (these are evidently the spermatids on the cytophore). He continues as follows: "Ces nouvelles formations qui rayonnent de la cellule-mere sont les vrais spermatozoides: leur flagellum se forme à la partie périphérique, tandis qu'ils sont encore fixé par l'autre extrémité; c'est apres qu'ils se sont détachés que leur tete s'atrophie comme l'on sait." These facts he describes as common to a number of species among them *Tænia expansa*, *i. e.*, *Moniezia expansa* as it is now known.

In describing the spermatozoa of *Tænia saginata* Leuckart[2] speaks of the "freilich kaum ausgezeichneten" head.

From all of these observations it is evident that where a distinct head is visible it is exceedingly minute and the observations of Salensky, Sommer, and Moniez seem to indicate that the spermatozoa of several species are without visible heads. The description of the collapse and degeneration of the nuclei by Sommer and the mention of atrophy of the head by Moniez appear to be somewhat closely in line with my own observations. But until other species have been examined with the aid of present cytological methods general conclusions are impossible. I am convinced, however, that if the spermatozoa of *Moniezia* possessed distinct, visibly differentiated heads I should have seen them in some cases at least. Comparative study of other species will undoubtedly prove of interest.

VII. *The Degeneration of Cell-Groups in the Testis.*

During almost the whole period of existence of the testis groups of cells undergo degeneration from time to time. Cells in any

[1] Moniez, "Sur les Spermatozoides des Cestodes," *Comptes Rendus*, 1878.
[2] Leuckart, "Die Parasiten des Menschen," 1879–1886.

stage of development from the spermatogonia to the developing spermatozoa except during the spireme stage are subject to this fate. The proportion of degenerating cell-groups varies greatly in different chains, proglottids and testes. In some chains only one or two cases of degeneration preceding the first appearance of the spireme stage have been observed. In others degenerating groups are found in almost every testis in the spireme period. During the earlier stages of the process the degenerating cells form rounded masses: later these break up and become distributed through the testis and are apparently absorbed by the cytoplasm of other cells. While it is impossible to assign positively a definite reason for this degeneration I am inclined to believe that it results from differences in physiological condition which may in turn be correlated with differences in nutrition. Careful examination of regions of rapid growth in many forms often shows a certain proportion of cells which are undergoing degeneration. Undoubtedly in such regions the intensity of certain stimuli or conditions carries some cells beyond the point where physiological equilibrium can be regained and they degenerate, serving perhaps as food for the others. There can be little doubt that the testis is a region of this sort. The great variation in the frequency of degeneration in different chains may indicate that it is connected with nutritive conditions. Apparently more cells are produced than can be sustained and some are eliminated.

The fact that no case of degeneration beginning during the spireme stage has been observed may be of some interest. It is not improbable that this stage is relatively independent of external conditions, *i. e.*, that a cell having entered this stage is capable of completing it without the intervention of external factors. To judge from appearances this stage is a readjustment or the establishment of a new condition of equilibrium in the cell and it may represent a reaction from previously existing conditions which have disturbed the previous equilibrium of the cell. There can be little doubt that in many respects the life of the cell possesses a cyclical character. One complex of processes or reactions continues until it brings about a reversal in reaction or initiates a different complex, etc.

That this degeneration has any connection with amitosis is

extremely improbable. In no case has a whole testis been found undergoing degeneration, yet in all the testes most of the divisions before spermatogenesis proper were amitotic and in the great majority the first divisions certainly were amitotic. As was suggested in the preceding section degeneration of cell-groups in post-spireme stages may be connected with the fragmentation of spermatocyte nuclei though this seems improbable, and moreover, it does not explain degeneration in pre-spireme stages. I believe, though I see no way of demonstrating it, that the method of origin of the cell-groups in the testis has no connection with their degeneration.

The degenerating cell-groups vary greatly in appearance according to the stage at which degeneration begins and the different stages of degeneration itself. In many cases, though not always, it is possible to determine from the appearance of the degenerating mass approximately the stage at which degeneration began. In some cases cells in the same stage of development undergo two different processes of degeneration.

Some of the characteristic forms and stages of degenerating cell groups are shown in the following figures: in these figures no attempt has been made to represent the cytoplasmic background. This varies somewhat in density and staining in different cases. Vacuoles and spaces are indicated by broken lines. The method of reproduction exaggerates the depth of shade in the more deeply staining portions. Fig. 51 (Pl. XV.) shows a small group of cells from a young testis in the first stages of degeneration. The first evidence of degeneration in these cases is a condensation of the cytoplasm and a massing together of the nuclei, and the degenerating group becomes quite distinct from other cells, usually lying in a space. Fig. 52 (Pl. XV.) shows a later stage of this form of degeneration; the nucleoli increase in size and stain very deeply, the nuclear membrane becomes indistinct, and the whole mass stains more intensely. Later, as shown in Fig. 53 (Pl. XV.), the mass breaks up into irregular deeply staining fragments and strands which are distributed through the testis and are often found in the cytoplasm of other cells surrounded by small vacuoles; a few of these fragments in the cytoplasm are shown in the figure.

Fig. 54 (Pl. XV.) represents a form of degeneration in cells in prespireme stages which sometimes occurs in old testes. Here the nuclei form irregular densely staining masses and finally the whole breaks up and is absorbed.

Fig. 55 (Pl. XV.) shows degeneration of a group of spermatid nuclei in a cytophore. The deeply staining granules and masses in the nucleus increase in number, the nuclear membrane breaks down, and the granules are distributed through the cytoplasm. In Fig. 56 (Pl. XV.) another form of spermatid degeneration is seen and a later stage in Fig. 57 (Pl. XV.). Fig. 58 (Pl. XV.) represents a still later stage: vacuoles usually containing a single granule still indicate the position of the nuclei; the mass stains only very faintly at this stage and seems to decrease gradually in size until finally it becomes imbedded in a cytophore and gradually disappears.

Fig. 59 (Pl. XVI.) represents a form of degeneration of the spermatids which usually occurs only after the spermatozoa have begun to develop. About the periphery of each nucleus a large amount of deeply staining substance develops and appears to flow toward the center of the cytophore. In Fig. 60 (Pl. XVI.) is shown a later stage of this form of degeneration. Here the cytoplasm stains rather more deeply than that of the normal cytophore, the deeply staining substance has disappeared entirely from the peripheral regions except in a few radiating strands and the positions of the nuclei are indicated only by vacuoles. In still later stages (Fig. 61, Pl. XVI.) the deeply staining substance gradually breaks up into granules (Fig. 64, *k*, Pl. XVI.), loses its staining power and finally disappears, and the whole cytophore becomes highly vacuolated, breaks up into irregular masses and shreds (Fig. 64 *l*, Pl. XVI.) and is apparently absorbed.

Other modifications of the process of degeneration are occasionally seen but these are the principal ones. The apparent variation which these processes exhibit is of some interest as indicating that differences in the processes of degeneration like differences in development are undoubtedly determined by differences in the condition of the cells or of the environment. At present, however, even a surmise as to the nature of these differences is of little value.

VIII. *The Full-Grown Testis.*

The testis continues to increase in size for a considerable time after spermatogenesis begins. Only a part of the spermatogonia enter the spireme stage at any one time, the others continuing to divide amitotically. After the appearance of the spermatogenetic divisions in a testis, I have never seen a case of mitosis in the spermatogonia, but amitoses are frequent. Figs. 62, *A*, 62, *B* (Pl. XVI.) represent groups of spermatogonia in full grown testes. In the same testes all stages of spermatogenesis and fully developed spermatozoa may be found. At this period the spermatogonia are usually found in small groups near the periphery. Figs. 63, *A*–63, *D* (Pl. XVI.), show cases of amitosis in spermatogonia from full grown testes, including nearly all the modifications of the process observed.

In Fig. 64 (Pl. XVI.), one half of a full-grown testis is shown on a scale half as large as that of the other figures. The different stages shown are as follows: at *a* is a group of spermatogonia still in the prespireme stage and showing one amitosis; *b* shows the earliest stages of the spireme, *c*, *c*, two groups with fully-developed spireme, while at *d* some cells are preparing for the first spermatocytic mitosis; at *e* is a cell in which the dyads are formed, part of a group which appears in adjoining sections; *f*, *f*, are cytophores with spermatid nuclei and developing spermatozoa; *g*, is a cytophore in which degeneration of the nuclei has begun, but the spermatozoa are still attached; at *h* is seen part of a bundle of free spermatozoa which can be followed in other sections; *k*, *k*, represent two degenerating cytophores in which the nuclei have already vanished: the shreds of cytoplasm and the debris from earlier cytophores are indicated at *l*. Although this one section does not show all the stages in the history of the cells, it serves to indicate the promiscuous distribution of different stages.

IX. *Conclusion.*

The point of chief importance in the present paper is the fact that typical mitosis and amitosis may appear together and apparently under identical conditions in the development of the male as well as of the female germ cells. The relative frequency of

the two forms of division varies in different chains, proglottids and regions. Observations and experiments to be described later will show very clearly, however, that amitosis as well as mitosis is an important factor in growth, not only in *Moniezia* but in many other forms and that in some cases at least either form of division may be changed into the other by altering the conditions.

These facts are of considerable importance as bearing upon certain hypotheses regarding the significance of the chromosomes. At present it seems improbable that the views held by certain authors regarding the individuality of the chromosomes can be reconciled with them. Extended discussion is, however, postponed until other facts have been presented.

The most important features in the development of the male germ cells in *Moniezia* are as follows :

The testes apparently arise from cells which are already differentiated as muscle-cells, as well as from other cells of the parenchyma. The earlier divisions are almost entirely amitotic, mitosis being rarely seen.

The growth of the testis up to the time when spermatogenesis proper begins is almost wholly by amitotic division. In the full-grown testis the remaining spermatogonia still continue to divide amitotically. After the spireme stage the spermatocytes follow two very different lines of development. In some of them typical dyads are formed and the two usual spermatogenetic mitoses follow : the spermatid nuclei are usually situated about the periphery of large masses of cytoplasm, cytophores formed by fusion of the spermatocytic cytoplasm, but may be isolated.

In the other spermatocytes the nucleus increases in size, the spireme breaks up into granules and masses and loses most of its staining power, the old nuclear membrane disappears, and new nuclear membranes form about small fragments of the chromatin : each spermatocyte may give rise to several small nuclei : in appearence these nuclei are indistinguishable from the spermatid nuclei produced mitotically. When first formed they are massed in groups in the interior of the cytophore about spaces which indicate the former positions of the spermatocyte nuclei. The nucleolus does not take part in this fragmentation but remains in the cytoplasm of the cytophore for some time. The nuclei thus

formed gradually make their way to the periphery of the cytophore and probably give rise to spermatozoa, though this cannot be demonstrated with absolute certainty.

Apparently only a part of the nucleus is involved in the formation of the anterior end of the spermatozoön in which no "head" is visible. The sperm-head is apparently represented by two granules in the nucleus, one peripheral, one more or less nearly central and a less deeply staining fiber which connects them, these being in most cases the only deeply staining portions of the nucleus. When development of the spermatozoön is completed the nuclear portion is apparently set free from the remainder of the nucleus by the degeneration of the latter.

Groups of cells in all stages of development except the spireme stage are frequently attacked by degenerative processes probably because of insufficient nutrition or exhaustion.

HULL ZOÖLOGICAL LABORATORY,
UNIVERSITY OF CHICAGO,
September, 1906.

EXPLANATION OF PLATES.

PLATE XI.

FIG. 14. *A*, *B*, the dyads grouped about the periphery of the nucleus. *M. expansa*.

FIG. 15. Dyads irregularly disposed in nucleus. *M. expansa*.

FIG. 16. *A–C*, dyads. *M. planissima*.

FIG. 17. Two dyads more highly magnified.

FIGS. 18, 19, 20, 21. Different stages of first spermatocytic mitosis.

FIG. 22. Two dyads in metaphase, more highly magnified.

FIG. 23. After the first spermatocytic division.

FIG. 24. Probably resting nuclei after first spermatocytic mitosis.

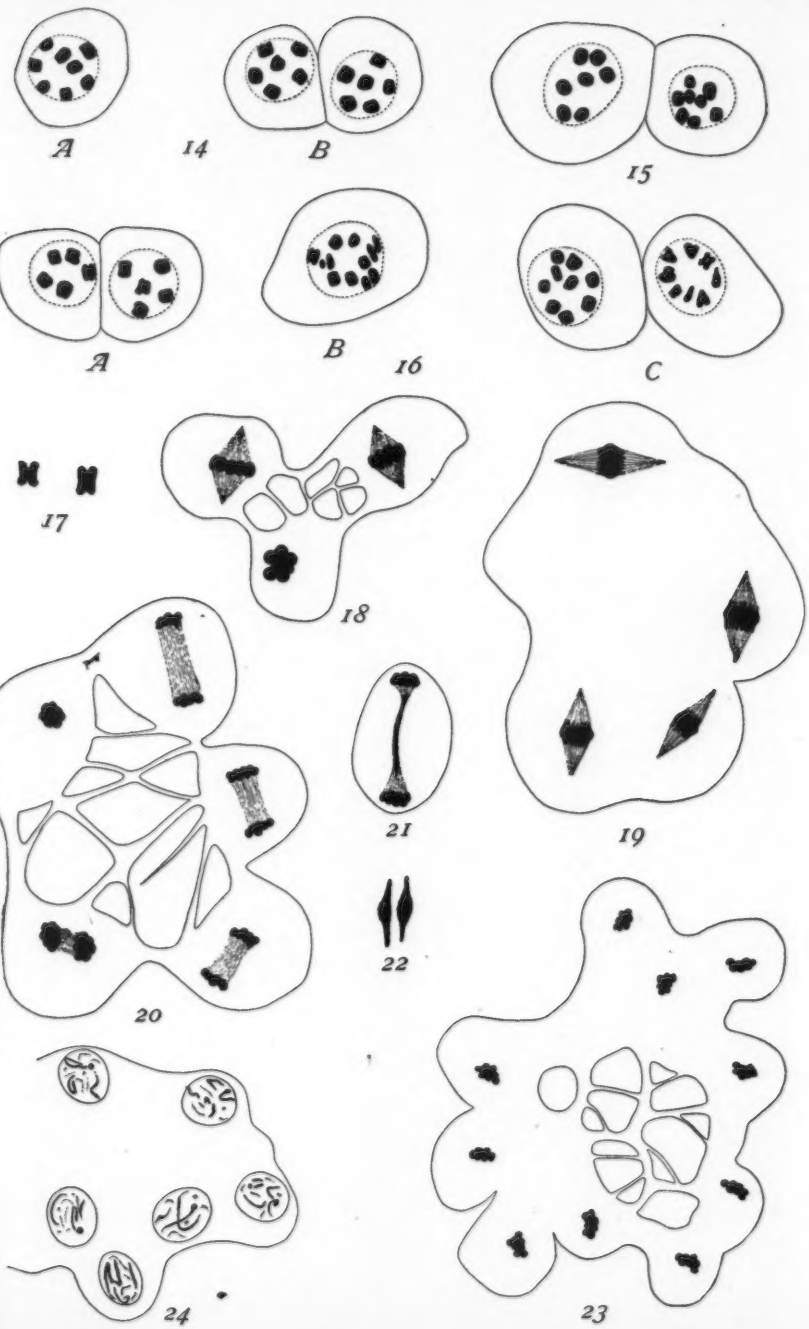
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PLATE XII.

FIGS. 25, 26. The second spermatocytic mitosis.
FIG. 27. *A–D*, early stages of fragmentation of nuclei of first spermatocytes.
FIG. 28. Fragmentation. One small nucleus forming.
FIG. 29. *A–E*, the formation of nuclei by fragmentation.

25
26
B
C
A
27
D
28
C
D
A
B
29
E

PLATE XIII.

FIG. 30. *A–C*, the formation of nuclei by fragmentation.

FIGS. 31–36. Nuclei and old nucleoli in the cytophores after fragmentation.

FIG. 37. Nuclei and old nucleolus after fragmentation with spireme stages adjoining.

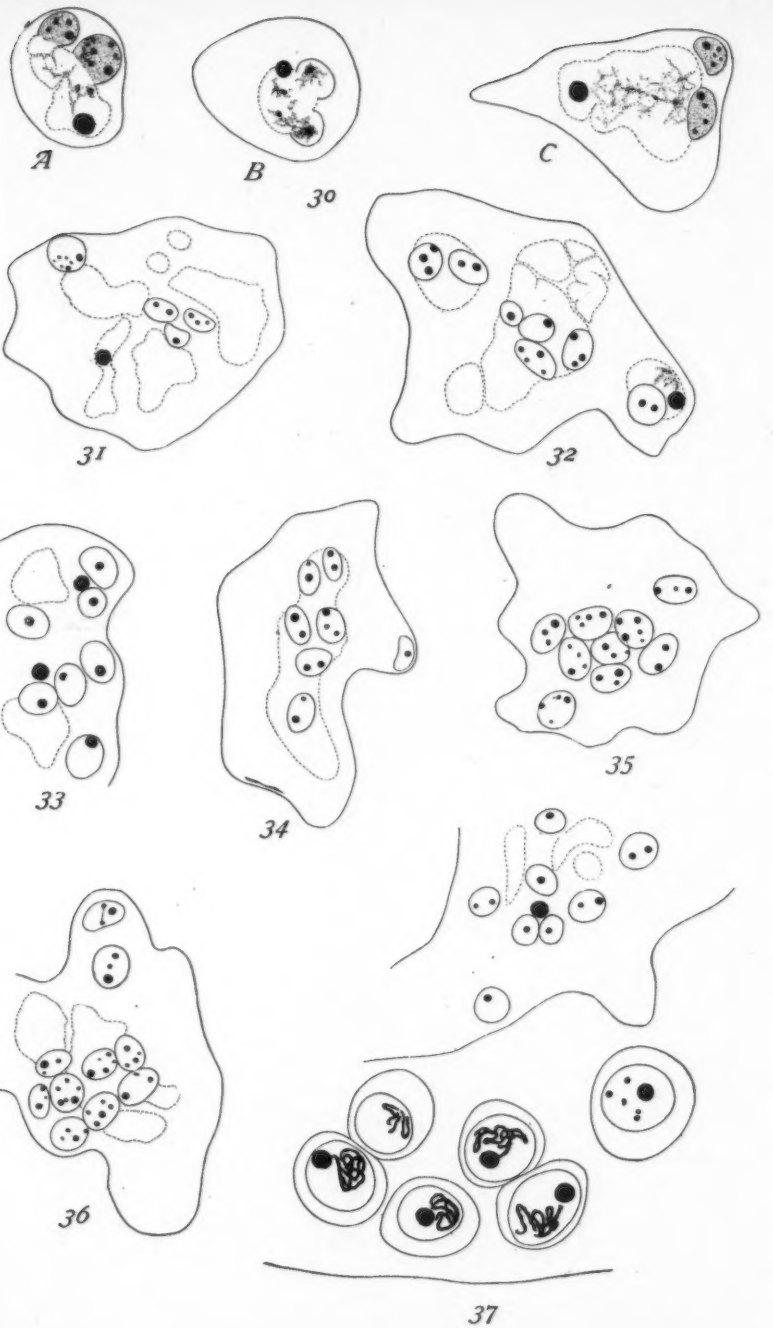
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PLATE XIV.

FIG. 38. Nuclei and old nucleolus after fragmentation with other stages adjoining.

FIG. 39. Probably migration of nuclei to periphery after fragmentation.

FIG. 40. Possible case of secondary fragmentation.

FIG. 41. A case of mitosis in a cytophore which was probably formed by fragmentation.

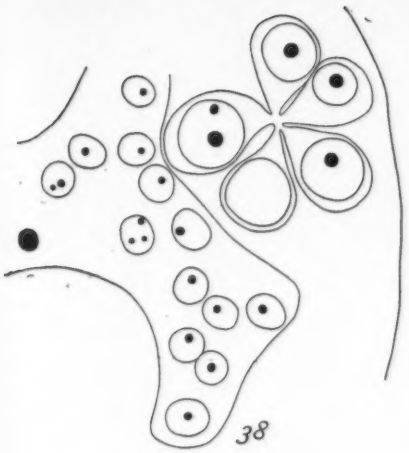
FIG. 42. Spermatid nuclei formed by mitosis.

FIG. 43. Spermatid nuclei.

FIGS. 44 and 45. Early stages in the development of the spermatozoa.

FIG. 46. Development of the spermatozoa.

FIG. 47. *A–E*, development of the spermatozoa after different methods of fixation and staining; *A*, *M. expansa*, sublimate and Delafield's hæmatoxylin; *B*, *M. expansa*, sublimate and iron-hæmatoxylin; *C*, *M. planissima*, chrom-oxalic and iron-hæmatoxylin; *D*, *M. expansa*, Hermann and iron-hæmatoxylin; *E*, *M. planissima*, sublimate and iron-hæmatoxylin, extraction stopped at an early stage.



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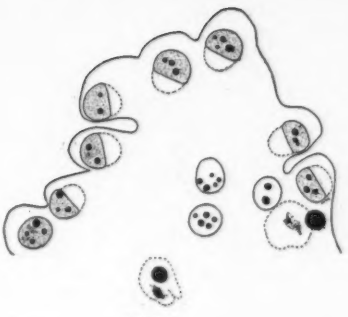

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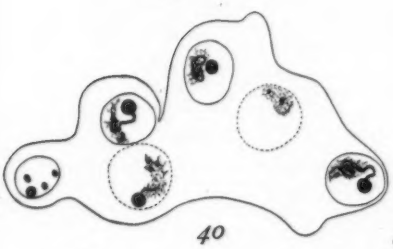

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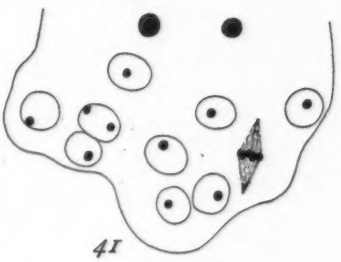

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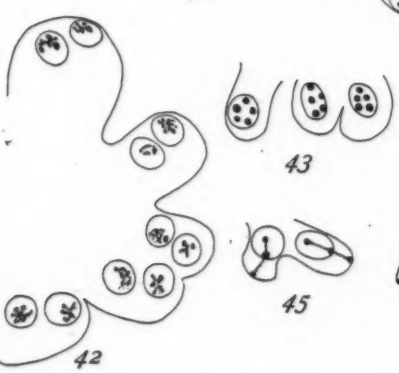

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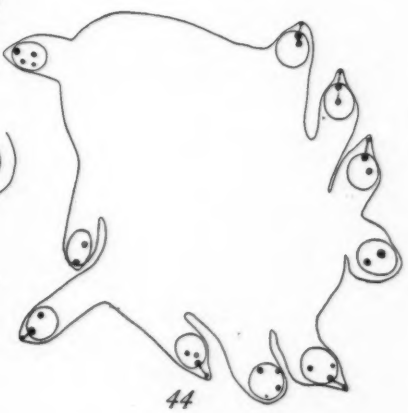

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A

B

47 C

D

E

PLATE XV.

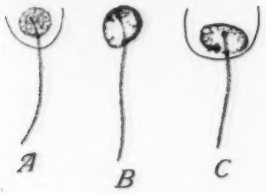
FIG. 48, *A–C*. The spermatozoön and the degenerating portions of the spermatid nucleus.

FIG. 49. A cytophore with spermatozoa and degenerating spermatid nuclei.

FIG. 50. Spermatozoa becoming free from degenerating cytophore.

FIGS. 51–54. Degeneration of cell groups in prespireme stages.

FIGS. 55–58. Degeneration of cell groups in spermatid stage.



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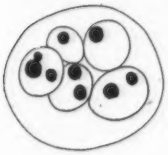

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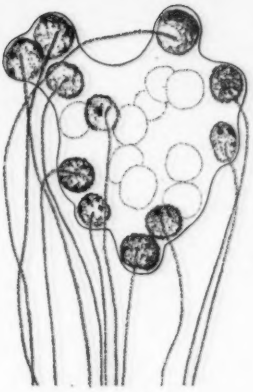

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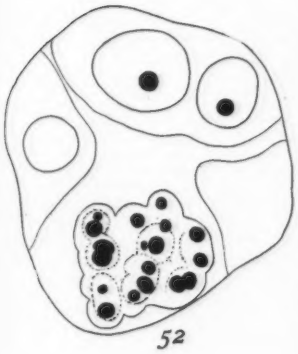

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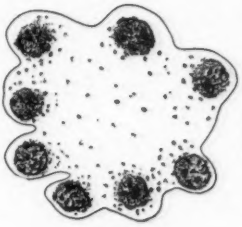

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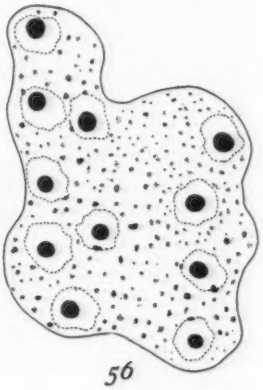

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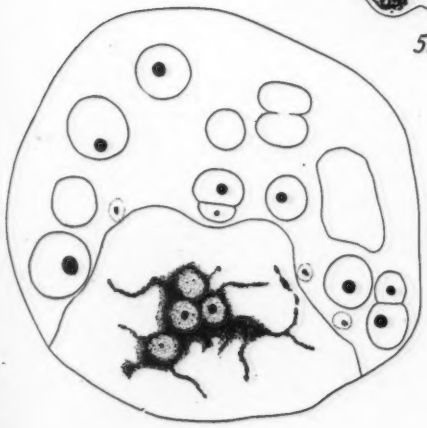

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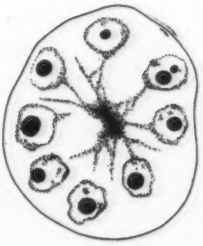

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PLATE XVI.

FIGS. 59, 60. One form of degeneration of cytophores after development of spermatozoa.

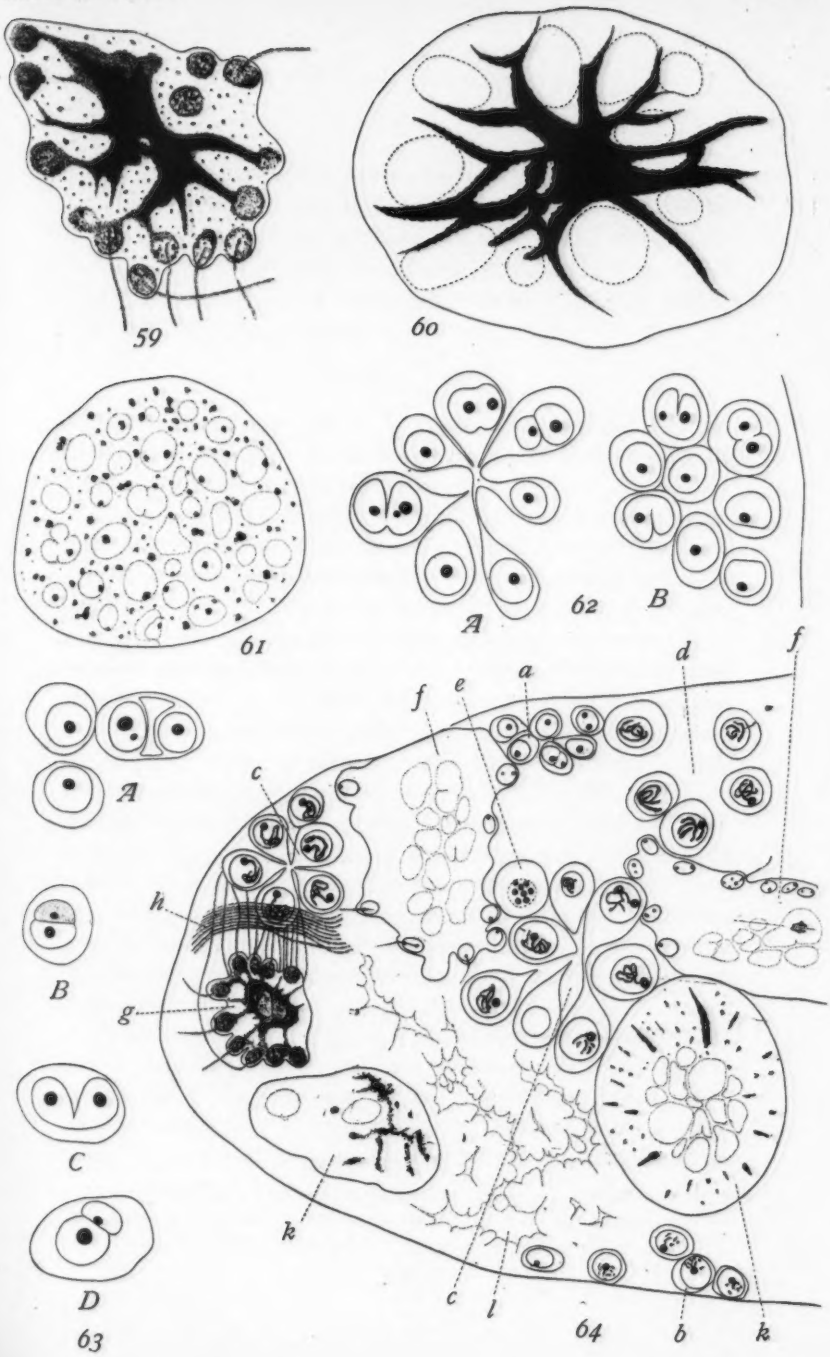
FIG. 61. Late stage of degenerating cytophore.

FIGS. 62, *A*, *B*; 63, *A–D*. Spermatogonia dividing amitotically; from full grown testes.

FIG. 64. Half of full grown testis; scale one half that of other figures; *a*, spermatogonia; *b*, early stages of spireme formation; *c*, *c*, spireme stage; *d*, preparation for first spermatocytic mitosis; *e*, dyads before first spermatocytic mitosis; *f*, *f*, cytophores with spermatids; *g*, cytophore with degenerating nuclei and spermatozoa; *h*, free spermatozoa; *k*, *k*, degenerating cytophores; *l*, shreds of protoplasm from earlier cytophores which have undergone degeneration.

The following figures are from *Moniezia expansa:* 1 *B*, 1 *D*, 3 *A*, 3 *B*, 3 *C*, 4 *B*, 4 *C*, 9 *D*, 10 *A*, 11 *A*, 11 *B*, 12 *A*, 13 *A*, 13 *B*, 14 *A*, 14 *B*, 15, 17, 18, 20, 21, 23, 26, 27 *D*, 28, 29 *E*, 30 *A*, 30 *C*, 31, 32, 34, 35, 36, 37, 38, 39, 40, 42, 44, 45, 46 47 *A*, 47 *B*, 47 *D*, 48 *A*, 48 *B*, 48 *C*, 49, 51, 55, 57, 58, 59, 60, 61, 62 *A*, 62 *B*, 63 *A*, 63 *B*, 63 *C*, 63 *D*, 64.

The others are from *M. planissima*.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THE CIRCULATORY AND NERVOUS SYSTEMS OF THE GIANT SCALLOP (PECTEN TENUICOSTATUS, MIGHELS), WITH REMARKS ON THE POSSIBLE ANCESTRY OF THE LAMELLIBRANCHIATA, AND ON A METHOD FOR MAKING SERIES OF ANATOMICAL DRAWINGS.

GILMAN A. DREW.

In considering any system of organs it is essential that we should bear in mind the modifications of the possessor of the organs, that adapt it to its particular life.

Pecten is one of the ablest swimmers among lamellibranchs. The whole structure of the animal is modified for this purpose. The valves have become rounded in outline, flattened, and comparatively light. The anterior adductor muscle has been lost, and the posterior adductor muscle, which is very powerful, is situated near the middle of the body. The cartilage has become well developed, so the shell may be opened quickly when the muscle relaxes, and the hinge line is straight, so there may be no unnecessary strains in opening and in closing the shell. Each gill is attached by one lamella only, so water in the temporary cloacal chamber may be thrown out without injuring the gills, and the gills and margins of the mantle are provided with muscles to withdraw them from the margins of the shell when the shell is closed. Furthermore the margins of the mantle are provided with infolded ridges and with circular muscles so it is possible to direct the current of water which issues from the shell in the required direction.

To fit the animal to a life of such activity, and to enable it to live in the comparatively exposed positions that it inhabits, an abundance of sense organs, tactile and probably visual, have been developed. These are placed in the most exposed positions, where they may give warning to their possessor, and are

[1] Free use has been made of both descriptions and figures published as No. 6 of the University of Maine Studies, under the title of "The Habits, Anatomy, and Embryology of the Giant Scallop (*Pecten tenuicostatus*, Mighels)."

accordingly borne along the margins of the lobes of the mantle.

It is not entirely certain what relationship *Pecten* bears to the usual form of lamellibranch as regards positions of parts. In lamellibranchs that are supplied with two practically equal adductor muscles, a line connecting the two adductors runs nearly lengthwise of the animal. In such a case the hinge line is more or less dorsal, one end is anterior, and the other posterior. When one of the muscles disappears, as is the case with *Pecten*, one of the landmarks disappears and it becomes more difficult to locate the direction of parts. Inasmuch as the hinge line is usually dorsal, it is very natural to look at the hinge line of this form as dorsal, and for matters of description it is convenient to so consider it. If, however, the position that the anterior adductor would have occupied, had it been retained, be considered, the position of the mouth, foot and heart indicate that it would have to be placed much nearer the hinge line than the present position of the posterior adductor muscle, the muscle that is retained. If this is the case, it becomes evident that the loss of the anterior adductor muscle has been accompanied by a general reduction of the anterior part of the body, so a large part of the body of *Pecten* is to be considered morphologically posterior. This supposition seems to be borne out by the nervous system, and the vascular system of the mantle, as well as by the extent and position of organs. In most forms the margin of each lobe of the mantle is supplied with a posterior and an anterior pallial nerve of approximately equal size. These nerves supply the muscles and sense organs of the margins, and, in many forms at least, unite with each other so they form a continuous connective between the cerebral and the visceral ganglia. In *Pecten*, not only is this the case, but the nerve in the margin of the mantle is joined at intervals for nearly its whole length by nerves from the visceral ganglion (Fig. 6). On the other hand, it is joined only in the region of the anterior ear by nerves from the cerebral ganglion. The visceral ganglia are the important ganglia of the animal, and both the cerebral and pedal ganglia are greatly reduced.

The blood is supplied to the mantle very largely by the posterior pallial arteries (Fig. 5). The anterior pallial arteries are

comparatively small, and while they are connected with the posterior pallial arteries, the size and character of the vessels indicates that the junction is probably very near the anterior ear.

Considering everything, it seems likely that the longitudinal axis of the body could be morphologically represented by a line drawn from near the hinge extremity of the anterior ear to the middle of the adductor muscle, and that a very small portion of the scallop is anterior.

Circulatory System.

The animal is large enough to allow one to successfully inject the chief vessels with starch or gelatin injecting mass, and then by dissection and microscopic preparations to trace the distribution of the vessels of the different organs and to determine quite definitely the course taken by the blood in its circulation.

The heart is a typical, symmetrical lamellibranch heart, with two auricles and one ventricle (Figs. 1 and 3), the latter perforated by the intestine which enters it near one end and leaves it near the other end (Fig. 2). Dorsally the ventricle is prolonged somewhat, posterior to the intestine, where the morphologically anterior aorta is given off, and ventrally to a less extent it is prolonged anterior to the intestine, where the much smaller morphologically posterior aorta is given off. The walls of the ventricle are of about even thickness throughout their extent, and are quite smooth outside and inside. The auricles join the ventricle on each side near its middle, are somewhat triangular in shape, with the most acute angle receiving blood from the gills and mantle at a point dorsal to the adductor muscle and directly ventral to, but some distance from, the cartilage. The opening of each auricle into the ventricle is near the middle of the side of the auricle that lies next to the ventricle and farthest away from the opening where the auricle receives its blood. The muscles around the openings of the auricles into the ventricle, and to a less extent around the openings through which the auricles receive blood, are well developed and must act as sphincters that tend to keep the blood from being regurgitated The walls of the auricles, unlike those of the ventricles, are roughened by pits that open into the cavities of the auricles.

Both auricles and ventricle are composed of interlacing muscle fibers, and are capable of great extension. In preserved specimens, the heart is usually contracted and is not very conspicuous. In such contracted hearts the cavities of auricles and ventricle are practically obliterated.

The heart lies in a somewhat triangular, spacious pericardial cavity that is dorsal to the posterior half of the adductor muscle, and ventral to the posterior portion of the liver. Posteriorly it is covered only by a somewhat thick, muscular membrane which separates it from the mantle chamber.

As already mentioned, two blood vessels leave the ventricle (Figs. 1 and 3), one from each end. Although they are not so placed in reference to the ways the terms are generally used in describing *Pecten*, the two ends correspond to the anterior and posterior ends of the ventricle in most forms of lamellibranchs. The posterior aorta is much the smaller of the two, leaves the heart ventral to the intestine (actually anterior to it) and divides immediately after leaving the heart, into two vessels, one of which, the smaller, follows along the intestine, supplying it and surrounding portions with blood. The other vessel turns almost at right angles upon leaving the aorta and enters the adductor muscle, where it divides into a system of vessels that supply the muscle with blood.

The anterior aorta is much larger than the posterior aorta, and supplies all of the remainder of the body. It leaves the ventricle dorsal to (actually posterior to) the intestine and very soon gives rise to a vessel which passes into and supplies the wall that separates the pericardial cavity from the mantle chamber. From the pericardium the anterior aorta follows along the postero-dorsal border of the liver to the base of the ear. Here it gives rise to the branch (Fig 3, *ppa*) which passes posteriorly to the extreme upper margin of the mantle that lines the ear, giving off along its course a number of branches, which supply this portion of the mantle. Here it divides into two vessels, a right and a left, each of which bends abruptly ventrally (Fig. 5, *ppa*) and follows along the margin of the respective mantle lobe about opposite the line of attachment of the infolded ridge of the mantle, alongside but external to the pallial nerve.

Very fine branches are given off from these vessels all along their courses, which further divide to form systems of capillary spaces that are finest and most numerous near the margins. Some of these capillary spaces are large enough to be injected with starch mass, and I have a preparation of the mantle lobe from which only the infolded ridge has been removed, that was dehydrated, cleared and mounted in balsam, in which the whole system of vessels can be traced. A gelatin mass not only fills the spaces mentioned, but passes out between the cells so that in sections it may be seen to be diffused throughout the tissue. This seems to hold good for all other parts of the body with the exception of the gills, in which organs the mass is more completely, but not entirely, confined to the blood spaces. The indication therefore is, that the blood spaces are not confined vessels, and that the blood functions as both blood and lymph. The posterior pallial vessel may be traced far anteriorly, gradually diminishing in size along its course. Here it finally joins the anterior pallial vessel. The anterior pallial artery (Fig. 3, *apa*) leaves the anterior aorta very near the cartilage and runs directly to the anterior border of the hinge region of the mantle, giving off vessels to this portion of the mantle on the way. Here it branches into right and left vessels, each of which bends abruptly ventrally (Fig. 5, *apa*) and pursues a course along the anterior border of the mantle similar to that taken by the posterior pallial artery at the other extremity of the animal.

Along the anterior border of the mantle, near the dorsal line, the vessel is rather small and slightly broken in its course. It may be possible that this represents the border line between the posterior and the anterior pallial arteries. There are other reasons for believing that a large share of the animal is morphologically equivalent to the posterior portions of other forms, and that the anterior portion is greatly reduced. This has received attention in another place.

Several vessels leave the anterior aorta to supply the liver and stomach. Most prominent among these is a vessel which leaves the aorta between the points of origin of the anterior and posterior pallial arteries. This bends out toward the left side of the liver, where, in injected specimens, it is very conspicuous, passes ven-

trally and sends branches to the major part of the liver and to the stomach.

A short distance in front of the cartilage the anterior aorta bends ventrally, passes through the liver and gives off a few small branches to it, sends a vessel to the palps in passing, and passes on to supply the foot and the visceral mass. The vessel that supplies the foot (Fig. 3, *fa*) leaves the aorta a short distance ventral to the mouth, passes along the body wall until the foot is reached, and extends into the foot along its dorsal border. Just before entering the foot this, the pedal artery, gives rise to a small vessel that passes posteriorly along the single retractor muscle of the foot, supplying it with blood. From the point of origin of the pedal artery the aorta extends into the visceral mass, following along the enlarged portion of the intestine that leads away from the stomach, and supplying this and other portions of the intestine and the reproductive organs with small and with large branches. The enlarged portion of the intestine that comes from the stomach is especially well supplied (compare Figs. 2 and 3), there being numerous small branches that are given off directly from the aorta, and large branches that follow along on the different sides of this portion of the intestine and likewise supply it with branches. A short distance ventral to the foot a large branch leaves the aorta and passes postero-ventrally to divide again and form small branches that supply the remaining loops of the intestine and the postero-ventral portions of the reproductive organs.

This completes what might be called the systemic arterial system. Beginning with the heart the system ends in the capillary spaces of the various organs. This system is most easily injected through the vessel in the suspensory membrane of the gills that is farthest from the adductor muscle (Fig. 1, *bv*), with a hypodermic syringe, injecting toward the heart. If a starch mass that will not pass through the capillary spaces is used, all of the vessels thus far described will be injected, as will also the veins that return blood from the gills, as this vessel is the one that returns blood from the gills to the heart. If a gelatin mass is used all of the systems may be injected, but as the injecting mass may pass out of the spaces, between the cells of the various organs, such injection does not aid in tracing the course of blood flow.

The systemic veins (Fig. 4) that collect the blood that is supplied by the systemic arteries, from the various organs of the body, may be injected from several different vessels. They may be injected by pushing the needle beneath the membrane that covers the posterior surface of the adductor muscle. A large blood space occupies this position, into which the needle is inserted and the mass injected fills the systemic veins. Another point from which these veins may be injected is from one of the superficial vessels of the visceral mass. These vessels are very conspicuous, and may be very easily picked up with the needle. Still another vessel is the vein that returns blood from the liver, which may be seen on the left side of the animal anterior to, but near the large artery that supplies the liver. Injecting any one of these vessels will to a greater or less extent inject the others, but there does not seem to be an entirely free communication between them. They all carry blood to the kidneys, and seem to empty into a common sinus on either side, that lies alongside the kidneys in the walls of the visceral mass. The sinuses of the two sides are connected beneath the adductor muscle, but it frequently happens that a complete injection of the system is not obtained from an injection from any one of the veins mentioned. Just where the obstruction lies in such cases has not been determined. It has been noticed that obstructions are more likely to be encountered in injecting from the veins of the visceral mass than in injecting from any of the others.

Inasmuch as blood spaces are cut in removing the muscle from the shell, it has been found desirable in injecting this system of vessels to wedge the valves open and to inject from the posterior surface of the adductor muscle. In injecting after the animal is removed, a considerable quantity of the injecting mass is sure to escape at the ends of the muscle.

The position of the veins may be seen in Fig. 4. A large vein comes from the liver, another from the foot, and the veins in the muscle unite to form a more or less definite sinus along the dorsal border of the muscle, and two smaller ones on the antero-ventral side of the muscle. These sinuses unite near the anterior ends of the kidneys. A series of vessels from the visceral mass unite along the borders of the kidneys and finally connect with these

sinuses. Most of the blood from all of these organs is distributed to the kidneys through systems of capillary spaces. The branching of these vessels is not conspicuous on the surface of the kidneys, but is better seen by cutting the kidneys open. That not all of the blood necessarily traverses the capillary spaces of the kidneys is indicated by the fact that injections of the systemic veins frequently fill the veins that carry the blood away from the kidneys as well as those leading to it. This is much more frequently the case when injecting from the posterior surface of the adductor muscle than when injecting from other places, and seems to be dependent upon a direct connection between the vessel in question and the sinuses on the antero-ventral surface of the adductor muscle near the dorsal ends of the kidneys.

Of the blood that leaves the heart, only that which goes to the mantle remains to be accounted for. This is collected and returned directly to the heart (Fig. 5, *pv.*)

All of the blood that leaves the kidneys is conducted to the gills. The blood from each kidney is collected into a sinus that runs along the border of the kidney that is applied to the adductor muscle. This sinus, which also seems to receive blood from the sinuses on the anterior and ventral surfaces of the adductor muscle, bends abruptly ventrally over the anterior end of the kidney and is continued on the lower border of the suspensory membrane of the gill (Fig. 1, *ba*) to the posterior end of the gill, supplying the gill with branches throughout its length.

Blood vessels leave the vessel that carries blood from the kidney, opposite each of the inter-lamellar junctions of each of the gills supported by the suspensory membrane. Each of these branches is continued along the free border of the membrane that forms the inter-lamellar junction (Fig. 7, *ba'*) until it reaches the free edge of the lamella, the edge that is not attached to the suspensory membrane. That is, if the branch supplies an outer gill, it leaves the suspensory membrane along the free border of an inter-lamellar junction and crosses over to the free border of the outer lamella of this gill. Here the vessel is continued down the enlarged, modified filament that is concerned in the formation of the inter-lamellar junction (Fig. 7, *ba''*) giving out side branches through each of the inter-filamentar junctions

(as long as these are composed of tissue that can carry blood vessels)[1] and so supplies the various filaments of the lamella. The blood thus distributed finds its way around the margin of the gill through small blood spaces and is continued up the other lamella of the gill, the blood of the small filaments being gradually collected through the vessels of the inter-filamentar junctions into the vessels of the large filaments (Fig. 7, *bv'*), and by these poured into a vessel that lies just beneath the vessel that supplies the gill and runs parallel with it (Fig. 1, *bv*). This vessel receives all of the blood from both of the gills of the side, and carries it directly to the corresponding auricle of the heart. Just before the vessel empties into the heart it receives a rather large vessel from the corresponding lobe of the mantle, which returns the blood that was sent to the mantle back of the heart.

To sum up the course of the circulation of the blood briefly, it will be seen that of the blood that leaves the heart only that which is sent to the mantle is returned to the heart after traversing a single set of capillary spaces; that a small portion of the blood sent to the adductor muscle (that which is collected by the sinuses on the antero-ventral portion of the muscle) may be returned after traversing two sets of capillaries — those of the adductor muscle and those of the gills; and that the greater portion is returned only after traversing three sets of capillaries — those of the general system, those of the kidneys, and those of the gills.

The reasons for this arrangement of the circulatory system are at least in part not hard to find. The blood which passes to the mantle loses some of its nourishing materials, but as the mantle lobes are thin and are bathed over such a large portion of their surfaces by a current of water, in which there is an abundance of dissolved oxygen, respiration, no doubt, takes place direct, and the blood has no need to pass through the gills to get a supply. Again the work of the mantle is not of such an active nature as to load the blood with nitrogenous wastes. It seems likely that the amount of nitrogenous waste in the blood that has traversed the mantle is so small that it

[1] The inter-filamentar junctions near the free margins of the gills are composed of cilia only.

would diminish the proportion of nitrogenous waste in the blood, if this blood were added to the blood that passes through the kidneys.

The blood that goes to the general system must in its progress lose a considerable portion of its oxygen, and in all portions except around the alimentary canal (where there is, of course, a decided gain) also food materials, and gain from the tissues a considerable amount of nitrogenous and carbonaceous wastes. It is then essential that such blood should go to the excretory and respiratory organs to get rid of these waste products and to gain oxygen. Inasmuch as the heart provides for but a single circulation it is necessary that the capillaries of these organs be traversed before the blood is returned to the heart. Why it is arranged so part of the blood may dodge the kidneys and be carried directly to the gills is not nearly so evident. Possibly the periodically great activity of the adductor muscle causes the blood to move through it so rapidly that the small kidneys cannot take care of it and properly perform their function, and the other channel is provided to carry the surplus away to the comparatively extensive gills where the increased flow can be taken care of with greater ease. It is, of course, essential that the amount of oxygen in the blood at such times shall not be reduced. It is at any rate evident that there is a possibility that part of the blood that is returned from the muscle, liver, etc., may not pass through the kidneys, for when starch injecting mass is injected through a vessel that carries blood from one of the kidneys to the gills, not only are the kidney and the gills injected, but part of the mass usually finds its way into the adductor muscle, liver, and other organs of the body.

The rate of the heart beat is slow, and as in other lamellibranchs is, no doubt, dependent upon the temperature of the animal as well as on other factors. The auricles and ventricle become very greatly distended during diastole, and contract so that their cavities are almost entirely obliterated in systole.

Nervous System.

The three pairs of ganglia that are usually found in lamellibranchs are present in this form, but they differ greatly in size and they are not all placed in the usual positions.

The cerebral ganglia (Fig. 6, *cg*) are placed some distance ventral to the mouth, just beneath the outer covering of the body. They, like the other ganglia, are yellowish in color, and may frequently be faintly seen through the covering of the body. Each cerebral ganglion is somewhat elliptical in outline with the long axis directed dorso-ventrally and has a rather distinct swelling on the ventral (actually anterior) and outer side (the side away from the median plane of the body) (Fig. 9, *cg*). The anterior end of each cerebral ganglion presents a forked appearance, due to the origin of two large nerve cords. The inner and ventral one of these two cords (Figs. 8 and 9, *cc*) is the commissure that joins the two cerebral ganglia. As the ganglia lie some distance ventral to the œsophagus, this commissure forms a long loop that passes dorsally around the œsophagus just posterior to the mouth. The outer and posterior of the two large cords that leave the anterior end of each ganglion is the anterior pallial nerve (Figs. 6, 8 and 9, *apn*). This runs parallel with the commissure as far as the œsophagus and is then continued along the side of the liver, and in the mantle, to the margin of the mantle in the region of the anterior ear of the shell, where it joins by several branches the circumpallial nerve (*cpn*) that follows along the margin of the mantle near the bases of the tentacles and eyes. The circumpallial nerve will receive attention later.

Between the points of origin of the cerebral commissure and the pallial nerve, a small nerve (Figs. 8 and 9, *pn*) leaves the ganglion to be continued dorsally, and to supply the labial palp.

From the inner, ventral surface of each cerebral ganglion, a little in front of the middle, the cerebro-pedal connective leaves to join the pedal ganglion of the same side. The cerebro-pedal connective is smaller near the cerebral than the pedal ganglion (Fig. 9, *cpc*) and bears a ganglionic swelling on its outer side very near the pedal ganglion.

In the acute angle formed by the surface of the cerebral ganglion with the cerebro-pedal connective, a small nerve (*otn*), the otocystic nerve, leaves the ganglion to be continued around the dorsal surface of the cerebro-pedal connective to the otocyst of the same side.

Posteriorly the cerebral ganglia taper rather gradually into the cerebro-visceral connectives, which run along the sides of the visceral mass very near the adductor muscle, until the visceral ganglia are reached.

The pedal ganglia lie very near each other (Fig. 9, *pg*), so the commissure that connects them is short and broad and presents ordinary ganglionic structure. They are separated from the cerebral ganglia only by a short interval, and lie anterior and slightly ventral to them, some distance dorsal to the base of the foot. They lie so near the surface that their color may frequently be distinguished through the body wall beneath the mouth. Two large nerves (*fn*) leave each pedal ganglion to be continued into the foot, where they supply the muscles of the foot and probably the byssal gland. The swellings on the cerebro-pedal connectives near the pedal ganglia have already been described. The otocystic nerves, which usually leave the cerebro-pedal connectives near the pedal ganglia, in this form originate directly from the cerebral ganglia near the point where the connectives leave the ganglia.

The visceral ganglia (Figs. 6, 8 and 10, *vg*) are by far the largest and most complicated of the ganglia, and from them nerves are sent to most parts of the body. They are situated on the antero-ventral surface of the adductor muscle, nearly opposite the external openings of the kidneys. They are imbedded in a mass of connective tissue and are fused to each other, so the commissure that connects them is nearly as broad as the ganglia themselves and shows ganglionic structure. The chief indication of the presence of a pair of ganglia is the arrangement of the nerves that leave them, and of the cerebro-visceral connectives that join them. The ganglia are divided into very definite regions, each of which is connected with definite bundles of nerve fibers and, no doubt, has a particular function to perform. I have not had time to make a detailed study of the structure and nerve tracts of the ganglia, but I am satisfied that there is much more complexity than is ordinarily attributed to the ganglia of lamellibranchs. The dorsal surfaces of the ganglia are quite smooth, but when seen from the ventral surface (Fig. 10) the regions that are indicated in the figure are always visible. On each cerebro-visceral

connective, just before it joins the ganglion proper, there is a ganglionic swelling (*x*) that supplies one of two roots of a nerve (Figs. 6, 8, and 10, *bn*) that leaves in an antero-dorsal direction along the border of the excretory organ, to bend ventrally and posteriorly in the suspensory membrane of the gills, and supply the gills of the corresponding side. Between the points where the cerebro-visceral connectives join the visceral ganglia on the ventral side, there are four rather distinct swellings, with three less distinct swellings posterior to them. Extending laterally from the outer side of each ganglion is a somewhat flattened ridge (Fig. 10, *y*) from which all of the pallial nerves from this ganglion originate. These nerves (Figs. 6 and 8, *ppn*) pass laterally, posteriorly and anteriorly along the surface of the adductor muscle, to meet the mantle lobes and to be continued to the margins, where they unite with the circumpallial nerves. It will be noticed that they unite with the circumpallial nerve at intervals throughout the greater length of this nerve. As the pallial nerves that leave the visceral ganglia in most forms pass directly to the posterior portion of the mantle, the distribution in this form may be looked upon as evidence that all of this portion of the mantle belongs morphologically to the posterior portion of the animal.

Other nerves leave the dorsal surface of the visceral ganglia near their posterior ends, and enter the adductor muscle directly. The nerves that supply the posterior division of the muscle are continued along the ventral surface of the anterior portion of the adductor muscle until this posterior portion is reached. Small nerves also leave the ventral side of the ganglia and penetrate the visceral mass.

All of the ganglia are well supplied with nerve cells, there being very many large polar cells present, but the number of the cells is far greater and their arrangement more complicated in the visceral than in any of the other ganglia.

Nerve cells are also to be found in the circumpallial nerves and in the branchial nerves. So abundant are the nerve cells in the circumpallial nerves that they assume the structure of ganglia. The nerves by which they are connected with the visceral and cerebral ganglia contain no ganglionic cells. From

the structural standpoint we would accordingly be justified in considering the circumpallial nerves as separate ganglia, and the nerves connecting them with the visceral and cerebral ganglia as connectives.

The circumpallial nerves of the two lobes of the mantle are connected with each other anteriorly and posteriorly near the hinge line (Fig. 8, *cpn*). They are not of constant diameter, but suddenly increase or diminish in size so that they have a rather irregular appearance. They lie just inside, that is, toward the median plane of the body, of the large pallial arteries that supply the mantle margin, about opposite the line of attachment of the infolded ridge. From them nerves are sent to the eyes and tentacles, to the infolded ridge and to the pallial muscles. Very likely the pallial muscles are partially supplied from the pallial nerves that come from the visceral ganglia, but of this I am not sure.

It seems probable that the ganglionic structure of these nerves has been developed to meet the needs of the very complex margins of the mantle. The development of ganglia in the immediate region of the sense organs is an indication of the ease with which such centers may be established when need arises.

The branchial nerves are supplied with ganglionic cells throughout their length. These are present not only along the borders of the gills, but from the points where the nerves originate to their extremities. The almost constant activity of the gills no doubt renders such an arrangement desirable. No other nerves or connectives in the body seem to be abundantly supplied with ganglion cells.

The whole nervous system is modified to meet the special needs of the animal. The cerebral and pedal ganglia are small, corresponding with the slight development of the anterior parts of the body and of the foot. The visceral ganglia are highly developed, corresponding to the excessive development of the parts that are supplied by these ganglia. Accessory centers have also been developed in the margins of the mantle and in the gills.

It seems that many students of Mollusca hold that the lamellibranch ganglia have been derived from a gastropod-like type, a

type that possesses at least one pair of ganglia, the pleural, that are not commonly found in lamellibranchs. This view seems to be based largely upon the acceptance of a hypothetical type for a primitive mollusk that seems to me to be a much better ancestor for the gastropods than for the other classes of the Mollusca.

Phylogeny.

The hypothetical primitive mollusk that has persistently been offered for our consideration, and has found its way into a number of text-books, among which is Lang's "Text-Book of Comparative Anatomy," has the dorsal portion of the body covered by a conical shell, the foot flattened and adapted for creeping, a head fold that may be protruded from beneath the shell, a pair of plumose gills, and a nervous system with at least four pairs of definite ganglia, cerebral, pleural, pedal and visceral. *Distinctly gastropod throughout.*

If the development of animals is to be considered of any importance in pointing their possible lines of descent, and as long as embryo chicks have gill arches our belief has good foundation, it would seem that in those mollusks whose eggs are not loaded with yolk, whose embryos are not modified for protection in brood pouches, and do not have long larval histories that call for special modifications to enable them to cope with enemies and to get food, the embryos might be suggestive.

The presence of unlimited food and protection always tend to destroy characters. Thus we find that parasitic forms may have entirely lost organs that must have been well developed before the animals took to parasitic lives. The presence of a quantity of yolk furthermore frequently must have mechanical effects on the developing embryo that cause direct modification. Again those embryos that pass through long larval histories exposed to the competition of forms that would eat their food and other forms that would eat them, must necessarily be exposed to the same evolutionary factors, whatever they may be, that adult animals are exposed to and we would accordingly expect adaptive modifications in them.

There are many lamellibranchs, and not a few gastropods, that do not seem to be seriously modified by any of these fac-

tors and when their embryos are examined every one must be struck with their close resemblances. These embryos would seem to point to a free swimming ancestral form that obtained its food by means of surface cilia.

The first living forms that made their appearance on the earth must have used non-living substances for food. What the nature of these substances were, whether they were of a comparatively simple nature, like those that are used by our green plants to-day, or whether they were of an entirely different nature, we have no means of knowing, but it is evident that their food was not alive.

Then came the discovery by some form that the protoplasm of other forms could be used for food. This must have been the first great factor that led to the competition of forms and called for the improvement of bodily machinery among living things, to aid in the struggle thus begun, the struggle to get food and to escape from being used as food. As Professor Brooks has indicated,[1] this would naturally lead to the discovery and colonization of the bottom of the ocean because of the greater advantages it offered both for capturing food and in affording means of protection. This introduces the further element into the competition, of some positions being far more favorable than others, and as the struggle for position increased, a struggle that has never ceased, the competition, especially between close relatives, must have become very severe.

These factors, with the struggle dependent upon them, must have caused changes in structure (in the improved machinery that aids forms in getting food and in keeping from being used as food) to change very rapidly and it seems very plausible that in a comparatively short time in those days when forms were of simple structure and this keen competition was begun, the foundations of the great types of animal structure were laid.

We know that among our earliest fossils are to be found both lamellibranchs and gastropods, and it is back in the earlier time that we must look for the changes that have resulted in the formation of these classes.

[1] Brooks, "The Origin of the Oldest Fossils and the Discovery of the Bottom of the Ocean," Smithsonian Report for 1894 (also Salpa).

We may possibly conceive that the ancestor of the Mollusca was among the early ones to recognize the advantages of the ocean bottom, and that its race soon developed a protective shell, if this had not started to form before it became a dweller on the bottom. The shell would offer protection, but would, because of weight, interfere with rapid movement. As enemies became able to get beneath its armor the shell became thickened and was made to cover the animal more completely, but the added weight interfered still more with rapid movement.

At this time we need not suppose that the animal had more than the very simplest nervous system, hardly more than that needed by a trocophore larva, for it would probably be dependent upon simple bands of cilia, or at the most a movable mouth portion, for getting its food. There is no reason for supposing that this animal had yet developed gills, or if gills were present they would hardly be more than simple folds of the mantle.

As competition became more severe, animals of this kind were in need of better protection, and it is possible to conceive that there might have been evolved two types, one that inclosed itself in a bivalve shell, crawled into the mud, and obtained its food by capturing the forms brought to it in a current of water of its own creation, the other, more like the *hypothetical primitive mollusk that has been described*, which retained a single shell and got its food by creeping over the bottom and picking it up directly. The first form would still have a simple head apparatus and would need new nervous centers only to provide for the mechanism necessary to crawl into the mud and the mechanisms necessary to create the current of water and capture the living forms from it. The second form would have a more complicated head apparatus and would need nervous centers to supply it and to supply the organ by means of which it was enabled to creep. In these differences in life, and in the consequent differences in structure, it seems reasonable to look for the differences in their nervous systems. If this conception is anything like true, from very early times there was no similarity in the method these two groups used in getting food. One has finally developed a remarkably satisfactory method of straining out living particles that serve it as food, from a current of water of its own formation, and

is thus able to leave little of its surface exposed to the attacks of enemies. The other has developed one of the most complicated of machines in connection with its mouth to aid it in getting food.

As the head apparatus of the one type has increased in complexity, there has been greater need of ganglia to supply it, but in the whole line of development of the other type there has been no complicated head apparatus. About all of the actual evidence that we have of the presence of pleural ganglia in lamellibranchs is that given by Pelseneer,[1] who finds in *Nucula* and some other forms, that each anterior ganglionic mass is so shaped that it is possible to consider it as two ganglionic masses, and further that the connective that runs from this mass to the pedal ganglion is connected with this mass by two roots. The interpretation that he has put on this is that the two apparent divisions of the ganglion represent respectively the cerebral and pleural ganglion, and that the roots of the connective represent the cerebro-pedal and pleuro-pedal connectives that have become fused before reaching the pedal ganglion. My own view, discussed in another paper[2] is that the apparent division into two ganglionic masses is superficial, and due to the swellings accompanying the origins of nerves, and that one of the cerebral ends of the connective may be the central end of the otocystic nerve which is fused for the greater part of its length with the connective, but, unlike most forms, is free near the ganglion. This view seemed to me most reasonable as Stempell[3] has found that in *Soleyma togata*, a supposed near relative of *Nucula*, the otocystic nerve arises directly from the cerebral ganglion and is separate from the connective throughout its length. So far as I know, the instance given by Stempell is the only one that has heretofore been reported where the otocystic nerves originate from the cerebral ganglia, and are free from the cerebro-pedal connectives throughout their length. *Pecten tenuicostatus* has the same arrangement. In this form the position of the ganglia, connectives and otocysts is such that it is a very simple matter for the

[1] Pelseneer, "Contribution à l'étude des Lamellibranchs," *Arch. de Biol.*, XI., 1891.

[2] Drew, "The Life-History of *Nucula delphinodonta*," *Quart. Jour. of Micro. Sci.*, Vol. 44, Part 3, New Series, 1901.

[3] Stempell, "Zur Anatomie von *Solemya togata*," *Zool. Jahrb.*, Bd. XIII., 1899.

otocystic nerves to make direct connection with the cerebral ganglia, but they do not join the ganglia at their nearest points. Instead they are continued around the connectives to join the ganglia in contact with, and posterior to them.

To me it seems probable that the separation into the two groups that have developed into the classes Lamellibranchiata and Gastropoda took place at an early date in the history of the Mollusca, probably before a complicated head apparatus was developed, and while the nervous system was of a very simple nature. If this was the case, we have no reason to search for pleural ganglia in lamellibranchs, for it is very probable that they never had them. In fact were ganglia ever present in this region in lamellibranchs, it would be more reasonable to view them as new formations for special purposes than as direct descendants from, and accordingly homologous with, the pleural ganglia of gastropods. The gastropod and lamellibranch are so different in structure and habits that we may reasonably expect important differences in their nervous systems. Gastropods and cephalopods possess accessory ganglia that have evidently been developed to perform special functions. That such centers may be comparatively easily developed is indicated by the fact that the circumpallial nerves of the scallop are essentially such centers. Is it not then more likely that pleural ganglia have been developed in the groups that need them than that lamellibranchs, which, so far as we know, have never been more complicated than they are to-day, should have formerly possessed these ganglia and have since quite uniformly lost them?

Anatomical Drawings.

It sometimes happens that in making a series of drawings intended to illustrate different organs of the same animal, considerable labor can be saved by using a combination of photograph and ink. The figures of the present paper illustrate this saving much better than is usually the case. To draw the margin of the mantle, with its large number of sense organs, requires both time and patience, and were it necessary to draw it for each of the figures where it necessarily occurs, one would be tempted to abandon it altogether.

It occurred to me, while engaged in drawing this margin, that possibly it could be photographed on a paper of a quality that would allow pen drawing and thus save redrawing it. After some trials a platinum paper was found that met the requirements but I was surprised to find how much blacker Higgins ink was than the blackest print I could make.

Evidently, however, any mark that would take at all in making a zinc etching would print the same color as the rest when being put through the press, so one of the poorest of these photographs was finished with Higgins ink and sent away to have a zinc etching made from it. The result was perfectly satisfactory. It will be seen that the margins on Figs. 1, 2, 3, 4, 6, 11, and 12 are all alike. The margin of Fig. 1 is the only one that was made with pen and ink. Fig. 11 is a print of a negative made from this margin before the rest of the animal was drawn. Taking a print similar to that shown in Fig. 11, with pen and ink there was drawn into it the organs shown in Fig. 12. Fig. 2, before the alimentary canal was added, was the figure from which the photograph resulting in Fig. 12 was taken. The margin of Fig. 12 is then a photograph of a photograph of an ink drawing. The original of Fig. 12 was then worked on to form Fig. 2 just as the original of Fig. 11 was worked into Fig. 1. Figs. 3, 4 and 6 are all worked onto prints similar to that shown in Fig. 12. In the original paper in which these figures were published a number of others were based on photographs in a similar way. The saving of time in the paper probably amounted to more than one half, and certainly may be of importance to others. I have no doubt that photographs may also be made the basis of brush work, but great care will be necessary in such cases in getting the proper printing value. While the figures accompanying this paper show no evidence that the photograph and the ink had different printing valves, they would have been very unsatisfactory had they been reproduced by some other processes.

Summary.

Circulatory System. — The large size of the animal makes it possible to inject the vascular system successfully. Blood from the mantle is returned immediately to the heart. Most of the

blood from other portions is carried to the kidneys, from which it is carried to the gills, and then back to the heart. A portion may dodge the kidneys and go to the gills. Blood seems to act both as blood and lymph. (See pp. 227–234 and Figs. 3, 4, 5 and 7.)

Nervous System. — The cerebral and pedal ganglia are small and somewhat removed from their usual positions. The visceral ganglia are very large and complicated in structure. The circumpallial nerves and the branchial nerves have ganglion cells throughout their length. The otocystic nerves originate directly from the cerebral ganglia. (See pp. 234–239 and Figs. 6, 8, 9 and 10.)

Phylogeny. — Ontogeny and the probable conditions that have resulted in the complication of structure, both seem to indicate that the division of the Mollusca into lamellibranchs and gastropods, took place at an early time, before the ancestors had attained much complexity of structure.

There seems to be no reason for believing that lamellibranchs ever had more complicated head machinery than they have at the present time. If this is true they probably have never had need of more anterior ganglia than they now generally have. (See pp. 239–243.)

Anatomical Drawings. — A combination of photographs and drawings may sometimes save much time and tedious work. (See pp. 243 and 244.)

UNIVERSITY OF MAINE,
ORONO, MAINE,
November 15, 1906.

PLATE XVII.

FIG. 1. Animal as seen from the left side with the left shell valve and mantle lobe removed and with a portion of the pericardial wall cut away. A few of the blood vessels are shown. Two thirds natural size.

FIG. 2. Animal as seen from the left side with the left shell valve and mantle lobe removed, with the alimentary canal shown. Two thirds natural size.

a, auricle; *ba*, branchial artery; *bv*, branchial vein; *c*, cartilage; *e*, excretory organ; *f*, foot; *fe*, free edge of the unattached lamella of the gill; *g*, gill; *i*, intestine; *lp*, labial palp; *m*, mantle; *pa*, posterior adductor muscle; *s*, stomach; *v*, ventricle; *vm*, visceral mass.

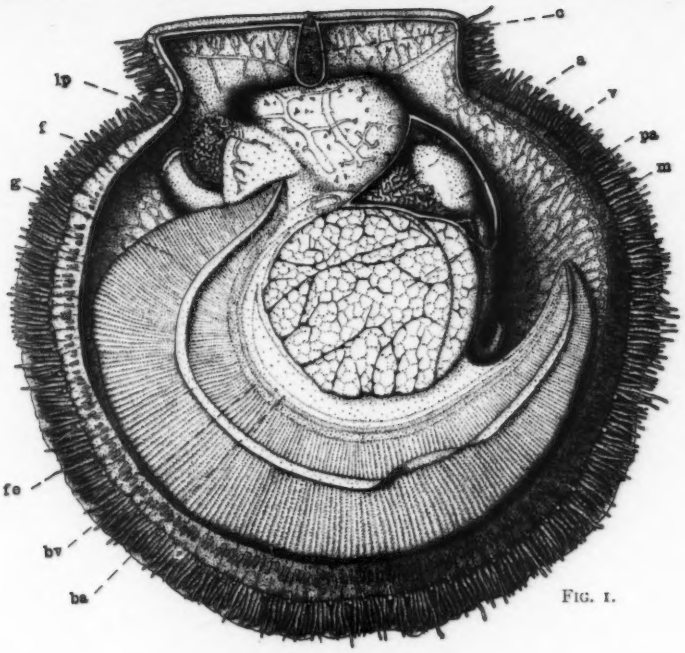

FIG. 1.

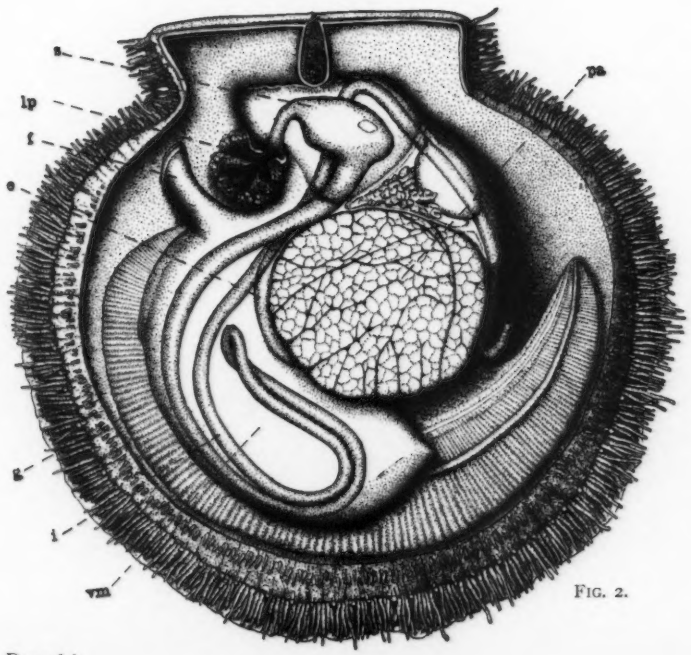

FIG. 2.

Drew del.

PLATE XVIII.

FIG. 3. Animal as seen from the left side with the left shell valve and mantle lobe removed. Drawn to show the arterial system of blood vessels. Two thirds natural size.

FIG. 4. Animal as seen from the left side with the left shell valve and mantle lobe removed. Drawn to show the systemic veins. Two thirds natural size.

a, auricle; *aa*, anterior aorta; *apa*, anterior pallial artery; *e*, excretory organ; *fa*, foot artery; *fv*, foot vein; *ha*, hepatic artery; *hv*, hepatic vein; *pa*, posterior adductor muscle; *paa*, posterior adductor artery; *pav*, posterior adductor vein; *ppa*, posterior pallial artery; *v*, ventricle; *va*, visceral arteries; *vm*, visceral mass.

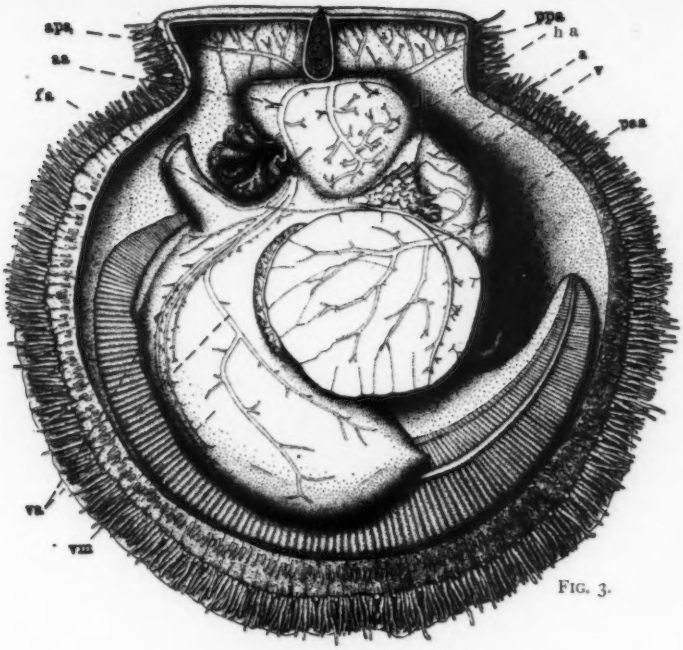

FIG. 3.

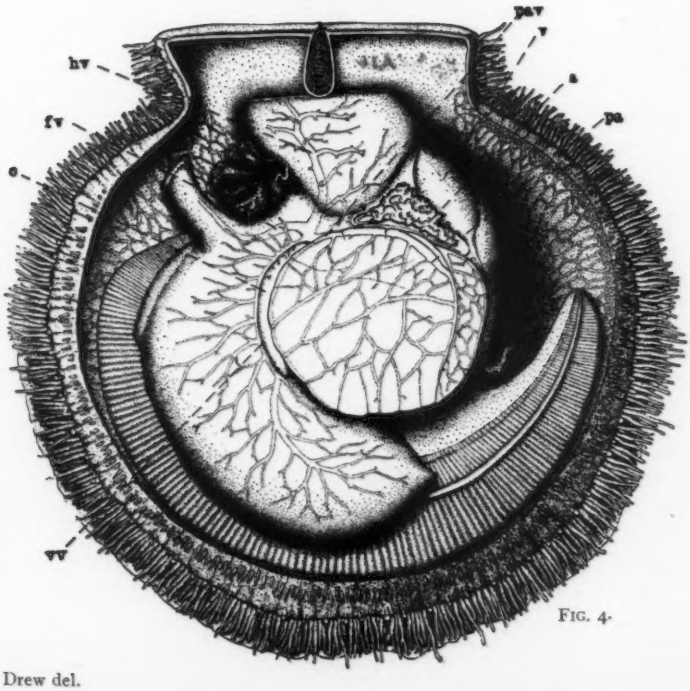

FIG. 4.

Drew del.

PLATE XIX.

FIG. 5. Outer surface of the left lobe of the mantle showing the arrangement of blood vessels. Two thirds natural size.

FIG. 6. Animal as seen from the left side with the left shell valve and mantle lobe removed. Drawn to show the nervous system. Two thirds natural size.

apa, anterior pallial artery; *apn*, anterior pallial nerve; *bn*, branchial nerve; *cc*, cerebral commissure; *cg*, cerebral ganglion; *cpn*, circumpallial nerve; *cvc*, cerebro-visceral connective; *ot*, otocyst; *pa*, posterior adductor muscle (anterior portion); *pa'*, posterior adductor muscle (posterior portion); *pg*, pedal ganglion; *ppa*, posterior pallial artery; *ppn*, posterior pallial nerve; *pv*, pallial vein; *vg*, visceral ganglion.

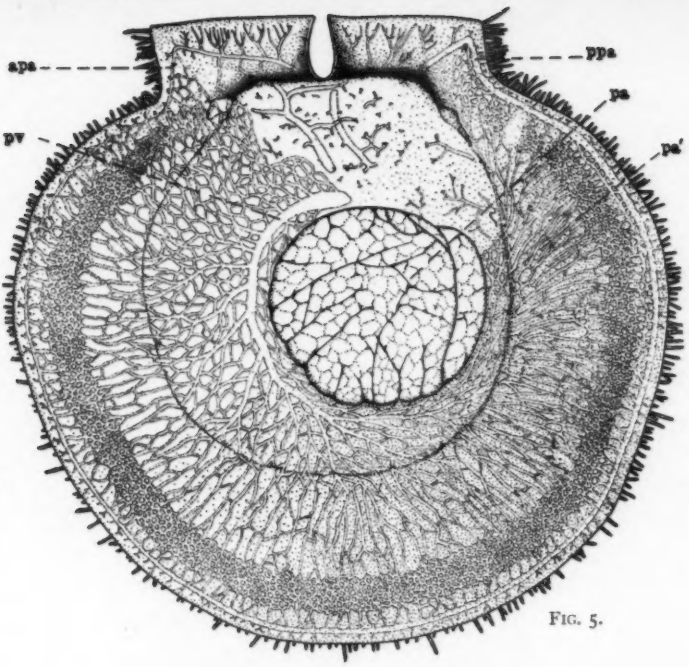

FIG. 5.

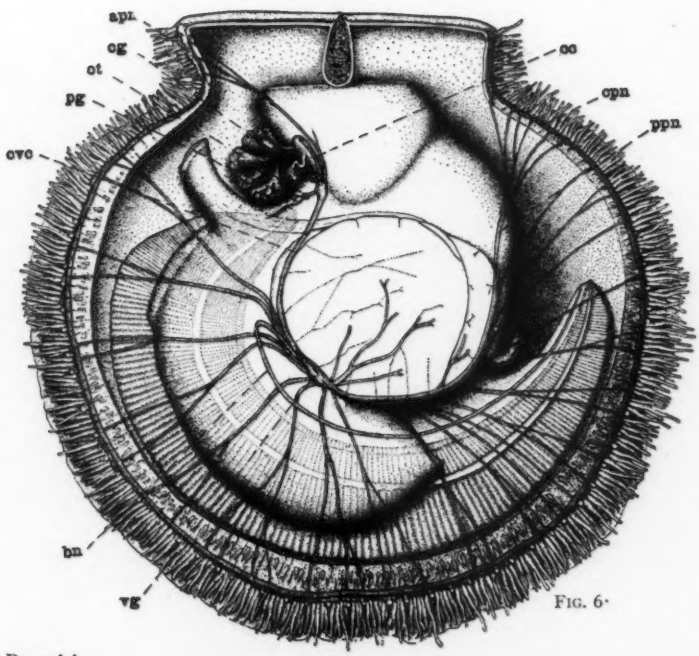

FIG. 6.

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PLATE XX.

FIG. 7. A portion of a gill showing the arrangement of parts. The figure indicates the inter-lamellar junctions cut at different levels. The further lamella is the one that was attached to the suspensory membrane and the vessel (*ba'*) was directly connected with the vessel that supplied the gill with blood (*ba*, Fig. 1). This vessel follows along the edge of the inter-lamellar junction to the free edge of the unattached lamella (the one on the side nearest the observer in the figure), where it bends back and passes down the modified filament as the vessel *ba''*. Branches are given off from this vessel through the inter-filamentar junctions to supply the filaments. The vessel *bv'* is the vessel into which the blood that has traversed the gill is collected. It in turn communicates with the vein of the gill (*bv*, Fig. 1). Magnified about seventy diameters.

ba', branch of the branchial artery; *ba''*, branch of the branchial artery in the modified filament; *bv'*, branch of the branchial vein; *cr*, chitinous rod; *gf*, gill filament; *iff*, inter-filamentar junction; *ilj*, inter-lamellar junction; *io*, inhalent ostium.

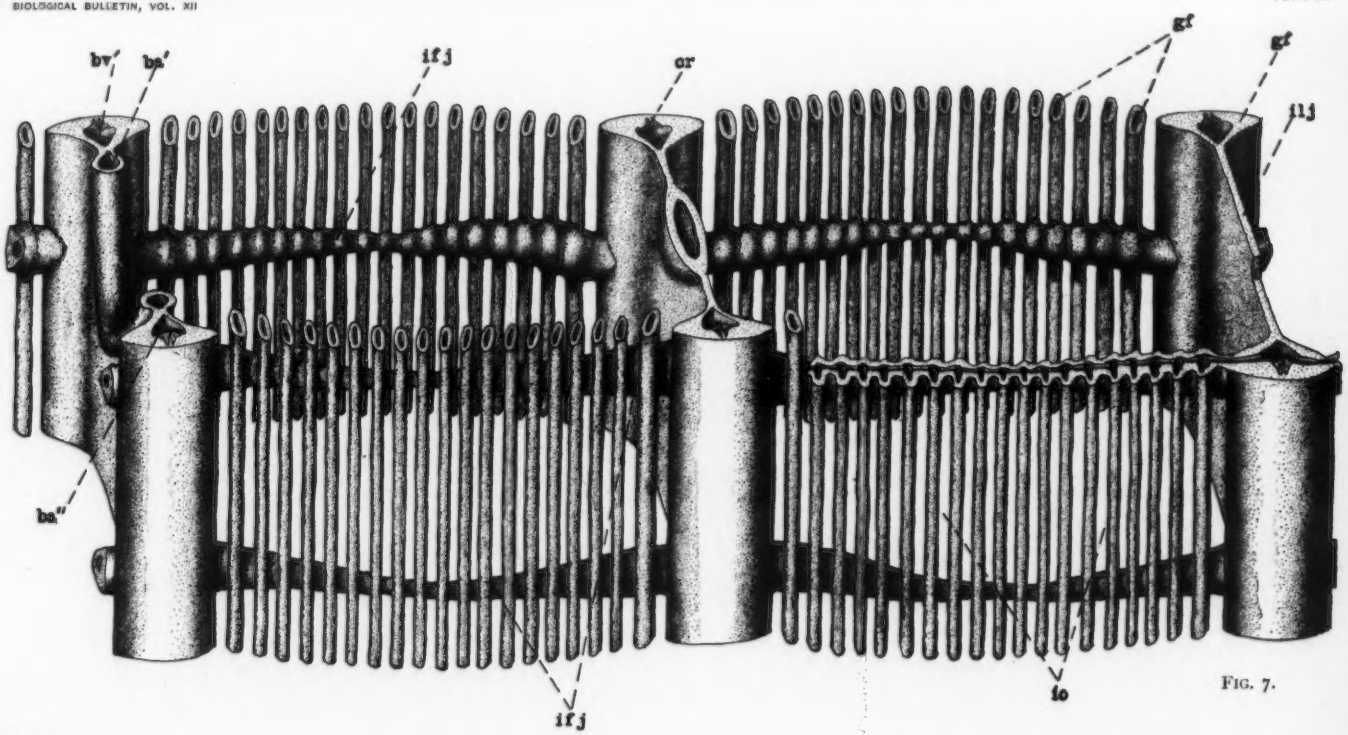

FIG. 7.

Drew del.

PLATE XXI.

Fig. 23. Nervous system as seen from in front and a little to one side. Natural size. (Diagrammatic.)

apn, anterior pallial nerve; *bn*, branchial nerve; *cc*, cerebral commissure; *cg*, cerebral ganglion; *cpc*, cerebro-pedal connective; *cpn*, circumpallial nerve; *cvc*, cerebro-visceral connective; *ot*, otocyst; *pg*, pedal ganglion; *pn*, palp nerve; *ppn*, posterior pallial nerve; *vg*, visceral ganglion.

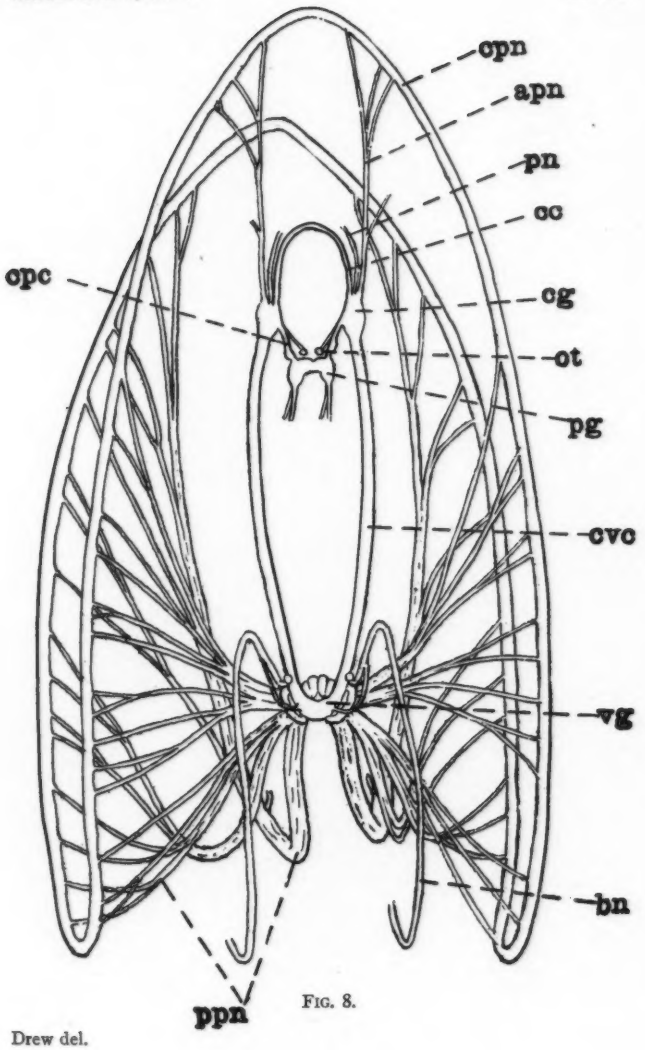

FIG. 8.

Drew del.

PLATE XXII.

Fig. 9. Cerebral and pedal ganglia with their nervous connections, as seen from the antero-ventral position. These ganglia and the otocysts lie in a mass of connective tissue and may be dissected out and mounted for study without injury Magnified about fifteen diameters.

Fig. 10. Visceral ganglia seen from the ventral side. These may easily be exposed for study by stripping the thin muscular covering from their ventral surfaces. They are hard to separate from the adductor muscle but they may be mounted with a thin piece of the muscle and studied in position. Magnified about fifteen diameters.

apn, anterior pallial nerve; *bn*, branchial nerve; *cc*, cerebral commissure; *cg*, cerebral ganglion; *cpc*, cerebro-pedal connective; *cvc*, cerebro-visceral connective; *fn*, foot nerve; *ot*, otocyst; *otc*, otocystic canal; *otn*, otocystic nerve; *pg*, pedal ganglion; *pn*, palp nerve; *ppn*, posterior pallial nerves; *x*, swelling on the visceral ganglion from which the anterior root of the branchial nerve originates; *y*, swelling on the visceral ganglion from which the posterior pallial nerves originate.

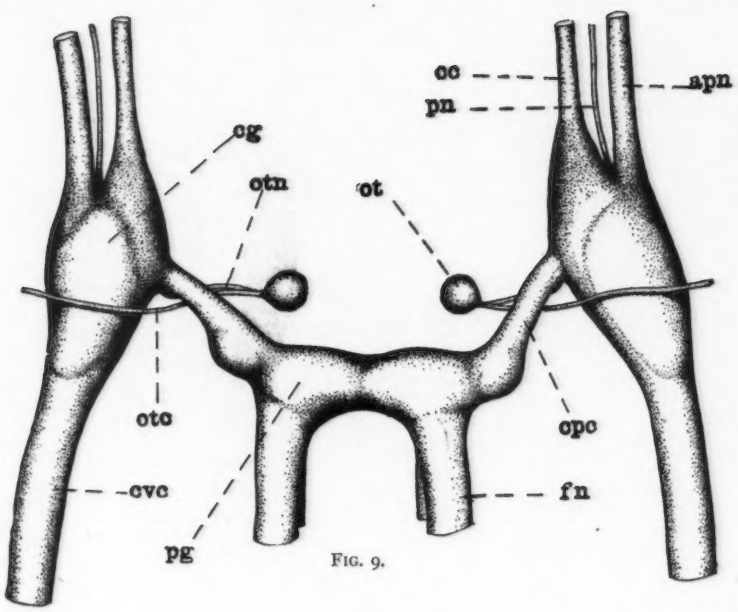

FIG. 9.

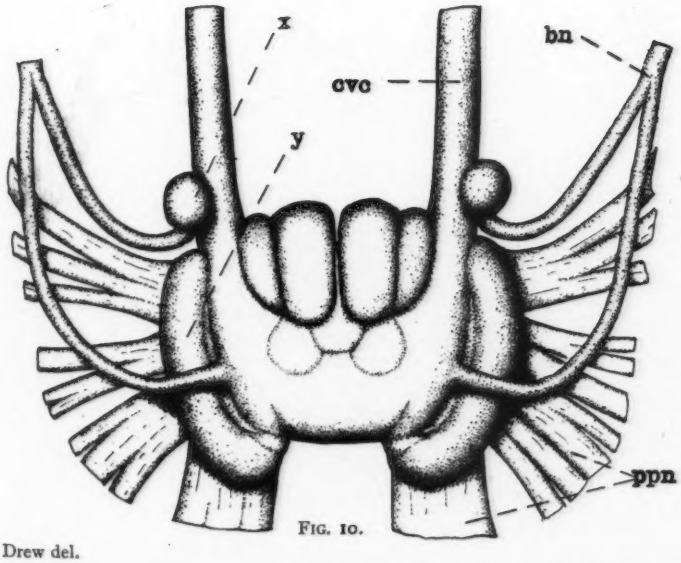

FIG. 10.

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PLATE XXIII.

Fig. 11. Etching made from a photograph of the margin of Fig. 1, before that figure had been completed. It will be noticed that the same margin occurs on all of the figures that show this portion of the mantle.

Fig. 12. Etching made from a photograph of a combination of a photograph and an ink drawing. The photograph was made from Fig. 2 before the alimentary canal had been worked in. Fig. 2 was drawn on a print like Fig. 11. Figs. 3, 4 and 6 are etchings of drawings made by adding various organs on prints like Fig. 12.

Fig. 11.

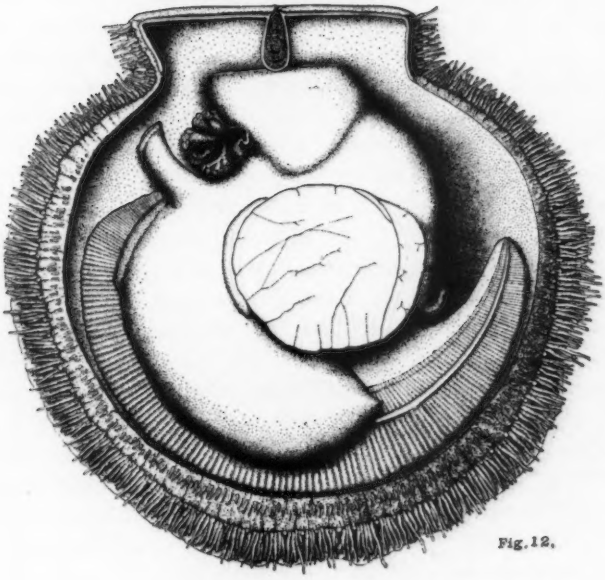

Fig. 12.

THE MATURATION OF THE MOUSE EGG.

WILLIAM B. KIRKHAM.

Sobotta ('95) after careful study of a very large number of preparations of the egg and ovary of the white mouse came to the conclusion that in nine tenths of these eggs the maturation processes involve the suppression of the first polar spindle, and the formation of only a single polar body. Gerlach ('06), after a study of preparations made at least as early as 1890, has revived Tafani's theory that in the majority of mouse eggs the second polar body is suppressed. Gerlach's conclusion is that when a spermatozoön enters an egg sometime after it has formed the second polar spindle, the second polar body fails to develop, and the spindle degenerates within the egg.

These results are at variance with the majority of opinions reached, before and since, by investigators of the eggs of other animals, vertebrate and invertebrate, and a reinvestigation of the maturation processes in the egg of the white mouse has brought it into line with most other metazoön eggs.

Material and Method. — The mice used have been killed during the period of most active breeding, namely, April, May, June and September, and serial sections made of the ovaries and Fallopian tubes. Ovulation, during the spring months, occurs very soon after parturition, independent of copulation, as observed by Rubaschkin ('05) in the guinea-pig.

When observed to be pregnant, the females were mated, and killed, some a few days or hours before parturition, others during that process, and still others at intervals from a few minutes to thirty hours after giving birth to a litter. The tissues were killed with a variety of the more generally used cytological fluids, and the following is a brief summary of the results obtained: All the ovaries contained some eggs with the second polar spindle and accompanied by the first polar body, and a majority of the series revealed ovarian eggs at the end of the spireme or with the first polar spindle. The eggs observed in the Fallopian tube fall into two main groups: those which had not been fertilized, and

therefore retained the second polar spindle — some being accompanied by the first polar body, more without it — and those which had been fertilized. The latter included stages from the entrance of the spermatozoön through the cleavage stages.

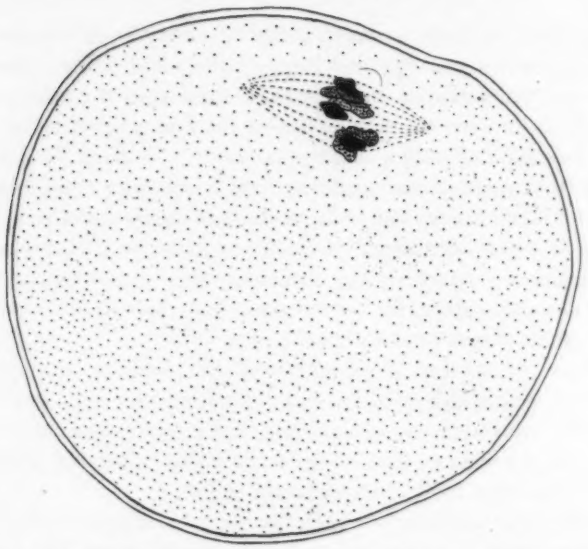

FIG. 1. Ovarian egg showing first polar spindle. Zona pellucida represented by double line. × 1200.

First Polar Spindle (Fig. 1). — The preparations in which there are stages immediately preceding the formation of the first polar spindle have not been fully studied, but there is evidence of a precocious division, the number of chromatin masses being between twelve and twenty-four.

The first polar spindle when first formed lies with its axis perpendicular to the radius of the egg, as found by Rubaschkin ('05) in the egg of the guinea-pig, and later one pole swings somewhat toward the center of the egg. The chromosomes of the first polar spindle are short and thick (Fig 2), and vary greatly in size. The spindle fibers come to more or less of a focus, and centrioles have often been seen at the poles of this spindle, where they are made up of several distinct, eccentrically placed granules.

First Polar Body (Figs. 3 and 5). — The study of many preparations reveals the following facts: None of the eggs in the Fallopian tube have failed to develop at least to the formation of the second polar spindle, and all the ovarian eggs which by their size, slightly denser protoplasm and large follicles appear to be nearly ripe, have already extruded the first polar body. The conclusion arrived at is, that apparently every egg which is capable of further development forms a first polar body within the ovary. This agrees with the observations of Rubaschkin ('05) upon the guinea-pig egg, and those of Van der Stricht ('01) upon the egg of a bat, *Vesperugo noctula.*

FIG. 2. Diagram of chromosomes in first polar spindle. Note great variation in size. Four more chromatin masses in adjacent sections.

This point established, it is next necessary to explain the disappearance of the first polar body in the majority of eggs seen in the Fallopian tube. The zona pellucida may persist in the mouse egg, undiminished, through the early cleavage stages, but in the majority of instances during the process of ovulation the first polar body is either forced through a weakened part of the zona, or frees itself by amœboid movements, and comes to lie outside the zona, as described and figured by Van der Stricht ('04).

The first polar body is usually oval in form, and is characterized, as found by Van der Stricht ('04) in the egg of *V. noctula*, by often possessing a little maturation spindle of its own, and in other instances having its chromosomes scattered. In some of these cases which possess a spindle, the first polar body would probably have divided mitotically, as observed by Sobotta ('95) in the mouse egg, and once by Rubaschkin ('05) in the egg of the guinea-pig. The polar bodies vary somewhat in size, and in one series of ovarian eggs there have been found first polar bodies of about four times the average volume. The number of chromosomes in the first polar body is twelve (dyads).

Second Polar Spindle (Fig. 3). — Immediately after the formation of the first polar body, the twelve dyads remaining in the

egg are drawn into the equator of a new spindle, split longitudinally, and the twenty-four daughter, univalent chromosomes

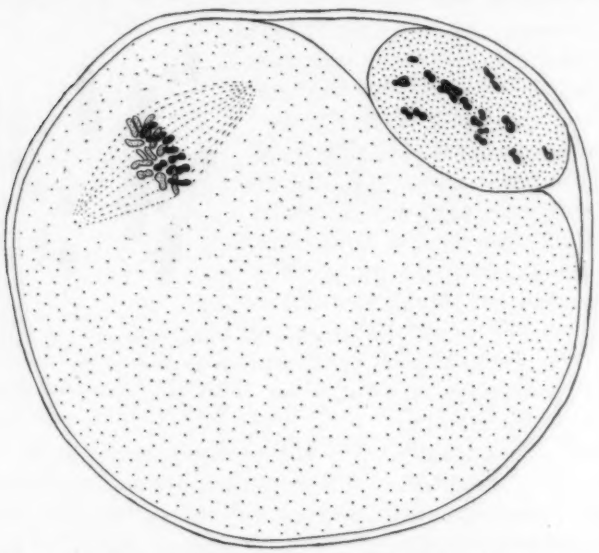

FIG. 3. Ovarian egg showing first polar body and second polar spindle. Seventeen masses of chromatin, some of which are undivided dyads, are scattered through the first polar body; twenty-four univalent chromosomes appear in the equator of the second polar spindle. Certain chromosomes have been added from adjacent sections. A minute centriole appears at each pole of the second spindle. The zona pellucida is represented by a double line. × 1200.

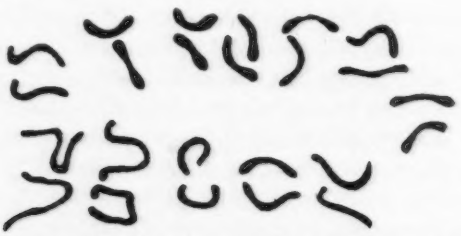

FIG. 4. Diagram of univalent chromosomes in second polar spindle, indicating difference in size.

lengthen out into filaments of various sizes (Fig. 4). Like the first polar spindle the second varies in size, and lies with its axis at

right angles to the radius of the egg, usually near the first polar body. Centrioles, similar to those described above for the first polar spindle, have frequently been observed in second polar spindles, and in some cases a few radiating aster fibers have been seen at the poles. In attempting to determine whether a given polar spindle is first or second, the character of the chromatin has always been found a positive guide.

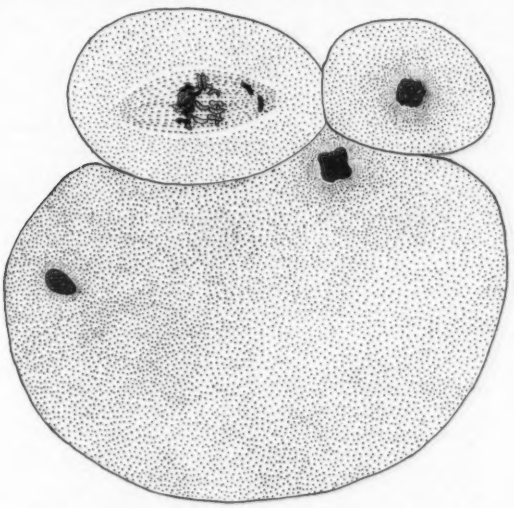

FIG. 5. Egg in Fallopian tube showing both polar bodies. Note spindle in first polar body. The sperm head appears at left, the female pronucleus at right, in the egg. × 1200.

Mature eggs which are retained within the ovary, together with such as are discharged and fail to be fertilized, degenerate with the second polar spindle, as found by Rubaschkin ('05) in the case of the guinea-pig egg.

Second Polar Body (Figs. 5 and 6). — Only one spermatozoön enters an egg, and it carries in most, if not all of its tail, a fact observed by Van der Stricht ('04) in the egg of *V. noctula*. When fertilized the egg at once forms its second polar body. This is more or less nearly spherical, smaller than the first polar body, and, as stated by Van der Stricht ('04) for *V. noctula*, generally

has its chromosomes gathered into a single compact mass. It quickly forms a resting nucleus, possessing compact masses of chromatin, and is usually the only polar body seen during the early cleavage stages. In one instance (Fig. 6.) a second polar body was observed which had just been constricted off, and in consequence showed the separate chromosomes, twelve in num-

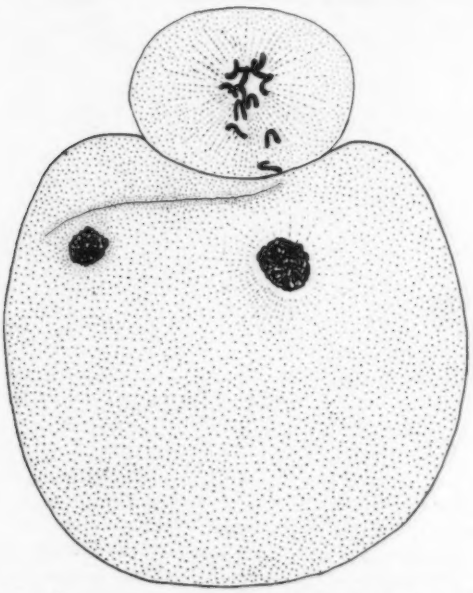

FIG. 6. Egg in Fallopian tube showing second polar body. First polar body has disappeared. At left in the egg is seen the sperm nucleus, and above it the separated tail of the spermatozoön; at right appears the egg nucleus, surrounded by delicate radiating fibers. × 1200.

ber, and another preparation showed the second polar body forming the resting nucleus.

The mouse egg is thus shown to be no exception to the general rule, that the maturation process in the metazoön egg involves the formation of two polar bodies.

In closing, I desire to express my gratitude, and great indebtedness to Professor Wesley R. Coe for his constant oversight and encouragement.

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ON THE ZOÖLOGICAL POSITION OF THE ALBINO RAT.[1]

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According to Leunis ('83) the black rat (*Mus rattus*) was known in Europe as early as the twelfth century, while the Encyclopedia Britannica (Olfield Thomas, '86) states the appearance of the black rat to be at least as early as the thirteenth century. Although the statements by the different writers as to the appearance of the black rat in Europe do not quite agree, yet it is clear that the arrival of the black rat was much earlier than that of the brown rat (*Mus norvegicus*)[2] which, according to various records, appeared in Europe at about the middle of the eighteenth century, or a little earlier.

Although both species of rats are described as originally natives of Central Asia, yet they are everywhere enemies. By the incessant competition between these two forms, the black rats were almost exterminated, first from Europe, and later from the greater part of North America, and at the end of the eighteenth century, the brown rats were alone found in abundance in these regions.

It is often stated that the white rat at present found in captivity, is the albino of *Mus rattus*. In support of this view there are a number of statements to be found in the older literature (Donndorff, 1792). (No effort has been made to examine the records previous to Linneus).

It is apparently on the basis of these records in the older literature that the current statements in popular natural histories and in encyclopedias are based.

On the other hand, in the zoölogical literature in the nineteenth century, there are numerous statements which refer to the albino rats as a variety of *Mus decumanus*.

[1] From the Wistar Institute of Anatomy and Biology at Philadelphia.

[2] *Mus norvegicus*, Erxleben = *Mus decumanus* Pall. of older Zoölogical Literature. *Norvegicus* has priority, and has come into general use within the last two or three years.

Von Fischer ('69) in a catalogue of the mammals of the St. Petersburg Government, makes the following statement:

"Die Wanderratte, *Mus decumanus* Pall. (russisch Krýssa — Krýssa heist eigentlich *Mus rattus*, diese art ist bekannt unter dem namen Passjúck) kommt ueberall massenhaft vor in allen Farben; schwartz, schmutziggrau bis rostgelb, weissgescheckt und auch ganz weiss. "Die Hausratte, *Mus rattus* L., habe ich nie gefangen, weshalb ich annehmen zu durfen glaube, dass diesse Ratte hier auch nicht vorkommt."

Von Fischer ('74) used a white *Mus norvegicus* in his experiments on the production of hybrids. Later Crampe ('85) also used a white *Mus norvegicus* in experiments of the same nature.

Haacke ('95) and Bateson ('03) studied the crosses between the white *Mus norvegicus* and the common brown rat. None of the authors, however, describe in detail the white forms which they employed.

Despite the general belief to the contrary, there are many reports in recent literature indicating that groups of *Mus rattus* are still to be found in a number of localities, both in Europe and the United States.

In the United States, *Mus rattus* is reported from Texas, Florida and other southern states, and also from Iowa. Rhoads ('03) reports a number of new localities in the States of Pennsylvania and New Jersey. It has been learned through Director Dr. Seitz that in Germany the black rat is present in large numbers in the buildings connected with the zoölogical garden in Frankfurt a/m.

It may be interesting to note that the occurrence of white rats in a wild state has been reported from two localities in Iowa, by students working in the neurological laboratory at the University of Chicago. There are no means of determining, however, whether these were albinos of the black or brown rat. From this review it is evident, therefore, that there are, or have been, at least two forms of albino rats.

Since 1893 a colony of albino rats has been maintained in the neurological laboratory at the University of Chicago, and in 1906 a similar colony was established at the Wistar Institute of Anatomy at Philadelphia.

These colonies have been recruited for the most part from the northern states of the Atlantic seaboard, but some specimens have come from as far south as Missouri. All the rats received from these various localities have appeared to be of the same variety, and have always bred true.

Heretofore, the specific similarity of the albinos and the other forms has been concluded from observation of the external characters only. Wishing more exact information as to the zoölogical relation of the rats composing these colonies, the present investigation was undertaken to determine whether we were dealing with an albino variety of *Mus rattus* or *Mus decumanus*.

Externally, *Mus rattus* is usually distinguished from *Mus norvegicus* by the following specific characters:

Mus rattus is smaller in size. The tail of *Mus rattus* is considerably longer than the body, while in *Mus norvegicus* it is either shorter or only slightly longer than the body, but not relatively as long as that of *Mus rattus*.

The following measurements, though incomplete, serve to indicate this relation:

TABLE SHOWING LENGTH OF BOBY AND OF TAIL.

Observer.	*Mus rattus.*			*Mus norvegicus.*		
	Length Body.	Length Tail.	No. of Obser.	No. of Obser.	Length Tail.	Length Body.
New International Encycl..	21 cm.					27 cm.
Leunis	16 cm.	19 cm.			19 cm.	24 cm.
Hatai				27 males	21 cm.	24 cm.

The general shape of the head (see Fig. 1) of *Mus rattus* is slender, the nose is sharper, and the ear is both wider and longer than in *Mus norvegicus*. It may be worth while to mention that the so-called Alexandrian rat (*Mus alexandrinus*) is said to have external characters similar to those of the black rat (*Mus rattus*) and these two species are only distinguished by their coloring, *Mus alexandrinus* having a brown colored coat.

If we compare the external bodily characters of the albino rat found in our rat colonies, with those of the brown rat, we are surprised by their close similarity. All these characters of the brown rat are also characters of the albino rats composing our

colonies. In other words, the common brown and our albino rats cannot be distinguished from one another by their external characters.

It is nevertheless true that the albino rats which we have examined, are smaller in size than the brown rats in the same localities. In fact, the absolute size of the albino rat is nearly intermediate between *Mus rattus* and *Mus norvegicus*. It is possible

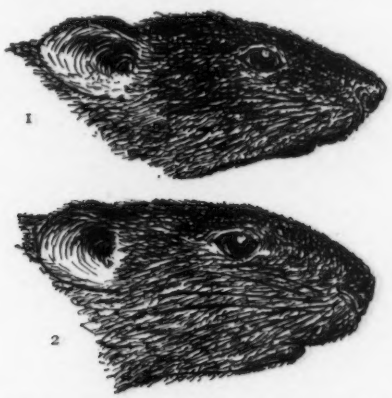

FIG. 1. Copied from "Encyclopedia Britannica," in order to show the shape of the heads of the brown and black rats. 1. *Mus rattus*. 2. *Mus norvegicus*.

that the confinement in which these albinos have been reared, accounts for their smaller size, as the result of lack of exercise and altered conditions of life. It is possible also that we have here a phenomenon similar to that described by Semper ('81) and De Varigny ('94) on snails, where the size of the animals diminished with the size of the vessels in which they were reared.

It was thought that the character of the skull might serve for a more exact distinction of the forms under discussion. We therefore examined and compared the skulls of *Mus rattus*, *Mus norvegicus*, and of the albinos.[1]

[1] In order to make this comparison, it was necessary to examine as many skulls as possible, and I am indebted to Professor J. A. Allen, American Museum of Natural History, at New York, Professor Elliot, Field Columbian Museum at Chicago, Dr. Greenman, The Wistar Institute of Anatomy at Philadelphia, and Professor Merriam, National Museum at Washington, for putting at my disposal various series of skulls, possessed by their several institutions.

To illustrate the differences found, both photographs and drawings have been made.

On comparing the skull of *Mus rattus* with the brown rat, the general unlikeness can be seen in Fig. 2.[1] The most noticeable difference is in the shape of the cranium.

When viewed from the dorsal aspect, the cranium of *Mus rattus* is oval in the outline, while that of *Mus norvegicus* is somewhat rectangular. Moreover, the dorsal aspect of the cranium in *Mus rattus* is decidedly convex, while in *Mus norvegicus* it is nearly flat. In *Mus rattus* the os nasale as compared to the entire length of the skull, is relatively shorter than *Mus norvegicus*. In *Mus rattus*, the outline of the os interparietale is somewhat semilunar in shape, while in *Mus decumanus* it is rectangular. In *Mus rattus*, the os parietale is broader as compared with its length, than in *Mus decumanus*. In *Mus rattus*, the foramen magnum is subcircular in outline, while in *Mus norvegicus* it is somewhat rectangular. On the ventral aspect of the skull, the large tympanic bullæ in *Mus rattus* are more conspicuous and eminent than in *Mus norvegicus*.

The junction point of the os basi-sphenoidale and os basi-occipitale is flat in *Mus rattus*, and protrudes in *Mus norvegicus*. The anterior end of the maxilla which forms the lateral wall of the infraorbital fissure, is blunter in *Mus rattus*, than in *Mus norvegicus*. The skulls of our albino rats are very similar in the above characters to those of *Mus norvegicus*, and the description of *Mus norvegicus* may be taken to apply to them.

In connection with the shape of the skulls, the determination of a cranial index has been made. The index used, was that obtained by dividing maximum width of the cranium by the length of the fronto-occipital line. (See Fig. 3.) On account of the small number of specimens measured, the accompanying table is to be considered as merely preliminary, but as it stands it shows a similarity in this index between *Mus norvegicus* and the albino rats, and a difference between these two forms and *Mus rattus*. The cranial index will be made the object of a more extended investigation.

[1] Care has been taken to use only the skulls of fully matured animals. See J. A. Allen ('94) and H. C. Merriam ('95).

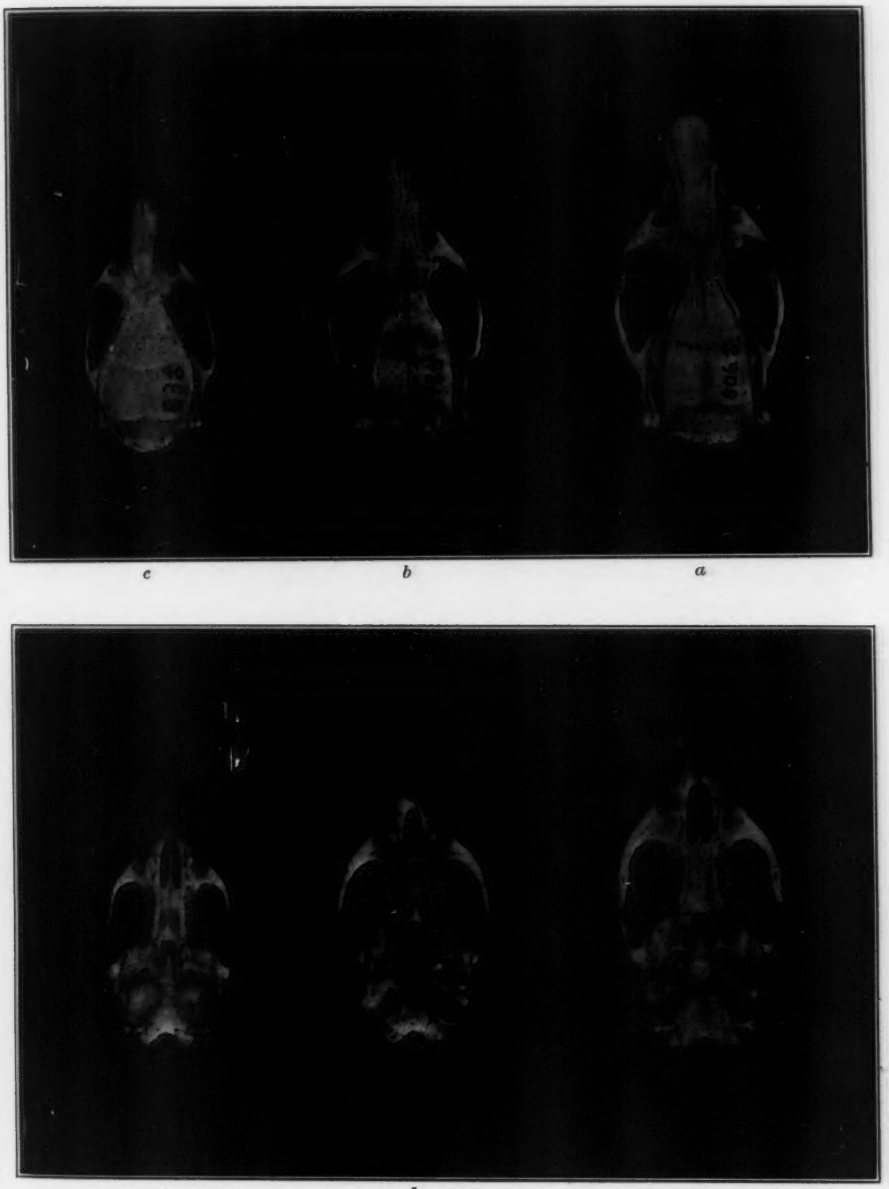

FIG. 2. Shows the skulls of *Mus norvegicus* (*a*), albino rat (*b*) and *Mus ratius* (*c*). The skulls were photographed from two different aspects, in order to show various views of the skulls for a comparison.

The upper row was taken from the dorsal aspect, and the lower from the ventral. The figures are about the natural size.

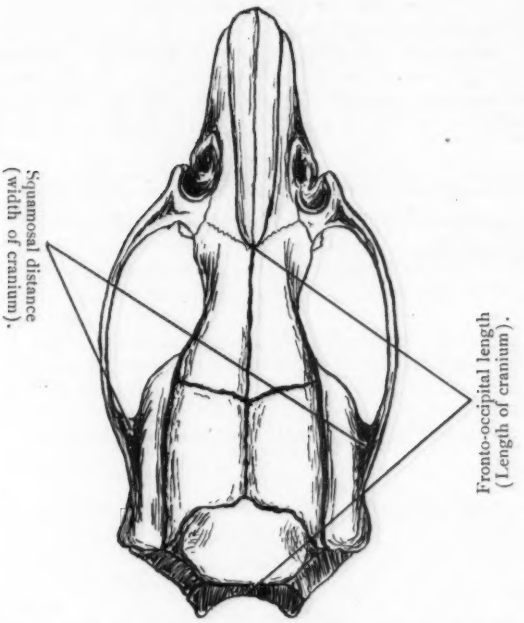

FIG. 3. (× two diameters.) The measurement of frontal-occipital length was determined in the following way:

Since the length measured from the tip of the nose to the posterior end of the inter-parietal bone, is not always equal to the length measured from the tip of the nose to the end of the occipital bone, both measurements were taken. First, the measurement from the tip of the nose to the end of the occipital bone, and second, that from the tip of the nose to the end of the inter-parietal bone. The difference thus obtained, was added to the length of the frontal-interparietal line, and the sum was called frontal-occipital length.

The width of the cranium was determined by taking a maximum width between the two points (right and left) where the zygomatic bones rest on the lateral walls of the cranium.

We conclude therefore, that the albino rats composing the colonies at Chicago and Philadelphia, are similar to *Mus norvegicus* in their bodily proportion, and in their cranial characters. They are however, smaller in size than the specimens of *Mus norvegicus* usually found.

TABLE SHOWING CRANIAL INDEX.

Males.	Cranial Index Average.	Extremes.	No. of Rats Used.
Mus rattus	.60	.58–.62	8
Mus norvegicus	.54	.51–.55	12
Albino rat	.54	.50–.56	12

Nevertheless this form is to be regarded as an albino variety of that species and to be designated *Mus norvegicus* var. *albus* (*oculis rubicundis*).

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NOTES ON THE BEHAVIOR OF SEA-ANEMONES.[1]

CHAS. W. HARGITT.

During the summer of 1901 while keeping a few sea-anemones in the aquarium for the purpose of studying their general habits, particularly those of feeding, my attention was drawn to the interesting phenomenon that certain species appeared more alert during the night, closing up more or less during the day. This was more noticeable in the large sand-anemone, *Eloactis producta*, whose peculiar habit of burrowing in the sand, enabled it to withdraw entirely when disturbed, or under other unfavorable conditions.

Having secured several specimens of this anemone they were placed in an aquarium, the bottom of which had been covered with sand to the depth of some six inches or more. The specimens, true to their habit, soon burrowed deeply in the sand, and lining the burrows with a slimy excretion they soon seemed quite at home. During the day they would be found with only the whorl of tentacles quietly protruding at the surface of the burrow, where their colors so closely conformed to that of the sand that the casual observer would hardly notice their presence. Going into the laboratory at night I was interested to see the specimens greatly extended, half of the body protruding beyond the burrows and tentacles raised in an attitude to seize passing prey. This was frequently observed afterward, and notes made of it at the time were recorded in which it was remarked that "these creatures are probably nocturnal in their habits."

At the same time I had under observation another anemone, *Sagartia leucolena*, a very common species about Woods Holl, and it was seen to migrate at times into darker portions of the aquarium, even creeping under bits of rock or other objects.

No further observations were made on the subject till the current summer. About a dozen specimens of *Eloactis* were collected and placed in the aquarium as before, and with the same

[1] Contributions from the Zoölogical Laboratory, Syracuse University.

result that such specimens as found sand proceeded to cover themselves as far as possible. In the light of current activity and interest in the matter of behavior it occurred to me to subject these creatures to a few experiments with a view of testing their reaction to light, and perhaps a few other environmental factors.

An examination of the available literature has brought to light but few instances in which any observations have been made concerning the behavior of actinians in relation to light. The Hertwig brothers, '79 ("Die Actinien Anatomisch und Histologisch," p. 191), cite brief observations made by Quatrefages on species of *Edwardsia* in 1842, and by Haime on *Cerianthus* in 1854, and include likewise brief references to their own observations on a deep sea-anemone, *Cladactis costæ*, in the Naples aquarium.

Quatrefages found that when a ray of light from a lamp was condensed upon the specimens by means of a lens they partially retracted. Haime observed that in bright sunlight species of *Cerianthus* contracted within their tubes and later expanded when the light became less intense. The Hertwigs record simply the fact the specimens during full daylight were more or less contracted and expanded as the light became less intense. "Im tageslicht zieht sie ihren Korper stark zusammen und erst wenn es zu dunkeln beginnt, dehnt sie sich auf das Vier- bis Funffache aus und entfaltet ihre Tentakeln, di zuvor eingezogen waren."

Jourdan has recorded a similar observation ("Les Sens chez Les Animaux Inferieurs," Paris, 1889), made upon a species of *Paractis* in which similar behavior was exhibited. "J'ai pu voir moi-même, sur des Actinies du genre Paractis, des manifestions evidentes de cette sensibilité spéciale. Des Orties de mer restent fermées aussi longtemps qu'on les expose à une lumière trop vive ; alles ne o'epanouissent que lorsqu'on les met à l'abri des rayons lumineux" (p. 221).

Eloactis producta. — My first observations were made to confirm those already cited, namely, to clearly demonstrate their nocturnal habit. Placed in the aquaria of the general laboratory, and in a few cases in smaller jars in my private laboratory,

their behavior was closely watched after the specimens had become adjusted to their new habitat. In this connection should be mentioned the fact, to be discussed later, that some specimens were much less prompt in burrowing, a few remaining more or less indifferently upon the surface of the sand and showing but slight attempts to bury themselves.

It only required a few observations to determine beyond any doubt that only in light of low intensity, such as twilight, or in the aquarium under the rather dim light of an incandescent lamp at some distance, did the specimens protrude their oral portions and tentacles and show any degree of activity. To further demonstrate that these seemingly nocturnal activities were not merely a periodic response made at more or less definite intervals, the following experiment was made. A tall glass jar, some twenty inches in depth, the lower third of which was filled with sand, in which had been placed several anemones some two days previous, was so placed on a laboratory table that it was freely exposed to the diffused light of the room. Over the jar was placed about mid forenoon, when the creatures were securely withdrawn in the burrows, a blackened chamber or dark hood, so arranged as to exclude more or less perfectly the light. Removing the hood at the end of an hour it was found that the creatures were quite extended as at night. And it was soon evident, that with the removal of the hood and the admission of light, they were at once aware of the change and promptly began to show signs of irritation, which ended within five minutes in every specimen having retracted into its tube. To make certain that the response had not been induced by some mechanical stimulus, such as the tremor of passing steps, or an accidental disturbance of the table or the water in the jar, the experiment was repeated within a half hour and under conditions which made it possible to observe the phases of the response.

Within fifteen minutes after the chamber had been placed over the jar it became quite evident that the change had been recognized by the specimens. This was shown first by the extension of the tentacles, and next by a slow protrusion of the oral region by degrees, till within about half an hour the body was extended an inch beyond the surface, as before. Again removing the

chamber and thus exposing the specimens to the light, within two minutes, indeed, almost immediately, they began to retract. This reaction is not sudden or general at once, as in such creatures as the earthworm, but begins in a somewhat indefinite movement of the body, accompanied by similar movements of the tentacles, followed very soon by a slow but definite retraction of the entire body within the tube, often including likewise the tentacles as well.

The experiment was later repeated in a room where it was possible to utilize direct sunlight. Under these conditions the reaction was much more energetic and definite, as might be expected. Variously modified, the experiments were performed repeatedly, perhaps fifty times, and with substantially the same results, though, as will be noted in a later connection, exhibiting variations of response. In some cases the reaction was so definite and prompt as to leave the impression on the observer that the creature was possessed of something akin to visual sensation. At other times the reactions were indefinite, sluggish, variable, and less convincing, though in the end resulting in the retraction of the specimen as before.

The following experiment was made to determine the extent of the sensory area, or in other words whether all portions of the body were similarly responsive to light. A specimen which had been quietly expanded on the surface of the sand for some time, being one of those which had shown less aptitude for burrowing, was so placed as to make it possible to reflect a narrow ray of light upon sharply defined parts of the body or tentacles. It was found that the oral region, including about one third of the body, was distinctly more sensitive than was any other. Light concentrated on the aboral portion seemed to have no effect at all, or so slight as to be indistinguishable. The tentacles were apparently less responsive than the immediately adjacent oral part of the body. This is slightly different from the condition found in *Sagartia modesta*, as will be noted later, and was a matter of some surprise, since the pigmentation of the tips of these organs might be thought to have some relation to sensory functions.

In a general way these results confirm the histological studies

of the Hertwigs (*op. cit.*, p. 22), as to the distribution of the sense cells in actinians. They also agree substantially with some of their experimental observations as to the unequal distribution of the sensory areas, though on this point they gave slight attention to the effect of light as a stimulus (*ibid.*, p. 190).

Sagartia modesta. — This anemone has much in common with the former species. It is a creature having its habitat in the sand just below or near low tide line. Like the former it takes somewhat readily to the artificial environment of the aquarium, though seems somewhat less hardy under these conditions. I first studied this species in its native haunt, having found several specimens on an accessible beach. I first found them just before twilight, and in the shadow of a large boulder which still further reduced the light, with the tentacles extended very much as in the case of *Eloactis;* the body was not protruded beyond the tube. Going again in the brightness of early morning they were not to be seen, no sign of tentacles even in the partially closed burrow. I made these observations several times, and concluded that they were probably also nocturnal.

Specimens were collected and taken to the laboratory and placed in the same general conditions as were the former species. Experiments similar to the former were performed, but with much less promptness or clearness in reactions. Placed under the dark chamber there was not the ready extension of the body as in *Eloactis*. Further, on removal of the hood the response was much less sharp and convincing, though quite evident. Placed on a table upon which a beam of sunlight could be reflected it was found when the ray was reflected upon the numerous tentacles that there was immediate reaction. It should be stated that in this species the tentacles are very numerous, even a hundred or more, and form a dense crown in expansion covering the oral region like an umbrella, while in the former species these organs are but twenty in number and rather short. In *Segartia* the tentacles seemed more sensitive than in the former species, or than the oral region, but this may be due in some measure to their numbers, and to the general relations they sustain to the oral portion of the body, especially the region just below the tentacles. Still the results agree again with the

views of the Hertwigs, as expressed in the following words: "Die Sinneszellen finden sich im Ektoderm der Mundscheibe und der Tentakeln, wie uns schien, überall ziemlich gleichmässig vor; nur an der Spitze der Tentakeln mochten sie vielleicht in grösserer Anzahl vorhanden sein" (*op. cit.*, p. 22).

Similar experiments were made on three other species of anemones, namely, *Sagartia leucolena*, *Sagartia luciæ*, and *Metridium marginatum*. These species are all more or less free, and variable as to habitat. The first, *S. leucolena*, is fairly common at various points along the shore-lines of the region of Vineyard Sound and southward. Its usual habitat seems to be under rocks near low tide, though taken also on the piles of docks. It seems to seek the under sides of rocks, or settles among masses of *Molgula*, sponges, etc., on piles, thus more or less secluded, and seldom seen by the casual observer.

On the other hand, *S. luciæ* seems to be equally at home almost anywhere in shallower pools, on fucus, piles of docks, etc., sometimes in shaded places, but oftener in the open sunlight on rocks, fucus, etc. About the same may be said of *Metridium*. While more common from deeper water than either of the others, it is yet quite common just below tide line on rocks, piles, etc.

The experiments on these species were made under the environment of the aquarium, but were sufficiently varied to give fairly satisfactory tests as to their reactions to this class of stimuli.

From what has been said as to the habitat just given it might be inferred that *Sagartia leucolena* would prove the more responsive to the tests, and such was found to be the case without exception, though as in the former cases, with considerable individual differences.

Verrill long ago pointed out that this species was more active when in dimly lighted aquaria, or at night. However, I have not found that specimens in the general light of the laboratory showed any very evident light reactions. But when an aquarium was placed in direct sunlight there was an almost uniform attempt on the part of specimens to escape from the direct rays. As a rule this was done by slowly creeping over the edge of the stone or shell into a less exposed position. Specimens which were in glass jars, and attached to the sides or bottoms of the jars, when

brought into direct sunlight soon closed up entirely, withdrawing even the tentacles, and assuming a more or less hemispherical shape. Taken from the direct light into the diffused light of the room they promptly expanded and remained so until again placed in the sunlight. This experiment was repeated again and again, and with substantially the same results. It was also found that the degree of contraction was very closely an expression of the degree of light intensity.

Many specimens were brought to the laboratory adhering to small rock fragments, bits of shells, etc. In a few cases when such specimens were exposed to direct light they would creep over to the shaded side of the rock, and during the night return to apparently the exact spot previously occupied. This might be taken to suggest some such sense of position as is known to be had by certain gasteropods; but the tests were not sufficiently numerous nor constant to warrant any definite statement.

With *Sagartia luciæ* and *Metridium* the case was very different, as might be expected. Specimens of these anemones placed under the same conditions as the former, indeed in many cases when occupying the same aquarium, were found to be almost without exception, quite indifferent to light. Placed for some time under a dark hood and suddenly exposed to direct sunlight there was not the slightest evidence that there was any sense of the change. The experiment was made in various ways. Sometimes as just suggested. Again, a beam of strong light was reflected directly on the specimen as it was quietly expanded on the table, but so far as *S. luciæ* was concerned, always and without exception, with negative results. Occasionally, though always doubtfully, *Metridium* would show some slight sensory movements of the tentacles. But specimens have been subjected to the reflection of a strong beam of light directly upon the oral surface for ten minutes at a time without the slightest response.

I have had a few specimens of *Edwardsia elegans* in the aquarium but for some reasons they did not seem at ease under these conditions, and exhibited no distinct evidence of any photic sensibility. I have seen but once any living specimens of *Cerianthus* at Woods Holl and then only under circumstances which rendered any observations impracticable. I regret therefore,

not to have been able to test the sensory behavior of these species.

The only other aspects of behavior which have been observed are those of feeding, and the very variable reactions concerned in tube-building.

Concerning the former my first experiments were made several years since. At that time I tested their feeding propensities by trying in various ways to induce them to take food. At various times during their aquarium life I tried to feed the creatures with bits of crab meat, bits of fish, clam, etc., but in no case was I able to induce the creatures to take the bait. During the present summer I observed that specimens of *Eloactis* which had been dug up and placed in a pail along with specimens of *Balanoglossus* were found devouring the latter alive. This was so unlike the former behavior that one was tempted to wonder whether they might have peculiarities of diet, and that their habitat on these sand flats, where likewise *Balanoglossus* has its home, might sustain some relation thereto. I therefore repeated the former experiment of offering them shreds of crab and fish meat and with the same negative results. I then tested them again with the *Balanoglossus* and found that it was taken quite readily by the same specimens which had refused the other bait. Leaving them for several days they were again tested with the same foods and with the same negative results. Having no specimens of *Balanoglossus* at hand some annelids, *Hydroides*, were offered them alive, and they were readily taken by three out of four tested.

No further qualitative tests were made along this line, but it would seem as if they were rather partial as to feeding habits, and particularly as to whether it be living or otherwise.

Limited tests were made as to their reaction to such substances as blood of crabs, clams, etc., but there seemed hardly any definite reactions indicative of olfactory, or gustatory sensibility. The swallowing reaction of *Eloactis* is much as in other species of actinians, namely that it consists largely of oral efforts. The tentacles play but little part in the reaction, though serving to press the food down upon the oral margins or lips. The swallowing act in these creatures involves something of a peristalsis of

the esophagus. It was observed in several instances that any considerable irritation of a specimen during the swallowing process was almost invariably followed by a reversion and ejection of the food. A worm three fourths swallowed would be ejected by a sort of antiperistalsis, which was more rapid than the swallowing had been.

From what has just been stated it need hardly be observed that attempts to feed specimens with bits of blotting paper, or other such materials, were uniformly negative in character.

The feeding experiments with other species were too limited to justify any special attention in this connection. In most cases no difficulty was encountered in inducing species of *Sagartia* to take food of almost any sort.

Burrowing Reaction. — Attention has been directed in an earlier connection to the fact that considerable variability is evident among various specimens as to the matter of burrowing, or tube-building. It may not be without some interest to briefly cite a few details along this line. It is one of the curious features in the activities of *Eloactis* that among a dozen specimens put into an aquarium the most remarkable difference of behavior in this respect may be seen. Most will show early signs of activity, and soon bury their bodies as completely as possible, and assume an erect position. Others appear to go through the efforts but in a most futile way. Left over night the aquarium will show in the tracks over the surface of the sand the varied movements made in this way. Still other specimens seem to show no effort whatever to burrow, but lie indifferently upon the surface, hardly showing signs of life except as they are stimulated by some means. This may continue somewhat indefinitely. But after a time a change may come over one of these sluggish specimens and it sets about constructing a burrow all at once, as it were, and within a night will have taken up the characteristic attitude of its kind. If now it be dug out and left again upon the sand it may promptly readjust itself again in a burrow, or it may remain for some days in the same indifferent aspect. Specimens which first bury themselves are usually prompt to build fresh burrows if dug out of the earlier ones.

The facts herein portrayed suggest several interesting inferences and inquiries by way of conclusion.

1. It seems clear that in the behavior of actinians toward light one is forced to recognize that certain species have sensory perceptions of photic stimuli quite as well defined as exist in such organisms as the earthworm, clam, etc. And while in this group of cœlenterates no such definite sensory organs are known as those found in many medusæ, the Hertwigs have described certain ectodermal cells which they have designated as sensory in function. It is not without some warrant that we may conclude that the various aspects of behavior under consideration are more or less definitely correlated with sensory structures and perhaps nerve cells.

2. Loeb, who has studied certain aspects of the behavior of *Cerianthus membranaceus* ("Physiology of the Brain," pp. 56–59), attributes them to the influence of two tropic forces, namely, geotropism and heliotropism. "Positive geotropism and positive stereotropism cause the Cerianthi to burrow in the sand vertically, and positive geotropism keeps them permanently in the burrow."

I have elsewhere shown the inadequacy of this explanation as applied to tube-dwelling annelids. I believe the facts under review may likewise be better understood and more consistently explained by other modes. Certainly the factor of light must be reckoned with as potent in the behavior of the several species studied. Again the variable behavior of these creatures in their burrowing habits is not easily accounted for on the usual theory of tropisms. Furthermore, it seems highly probable that in some cases the food-taking habit may sustain a relation to the general tube-dwelling habit.

3. Finally, as one considers the interesting facts as to the distribution of these light-reacting anemones the foregoing inferences are strongly corroborated. It is not necessary to review these facts in detail. It will be recalled that the observations of Quatrefages and Haime, already cited, had to do with species of *Cerianthus* and *Edwardsia* both of burrowing habit. Those of the Hertwigs were made on a species of *Cladactis*, an inhabitant of the deep sea. The observations of Jourdan were made on a species of *Paractis*, whose habit is not given, though species of this genus taken by the Challenger Expedition were also from the deep sea.

Of the species which have come under my own observations as light-perceptive, two are tube-dwelling, and one free-living, but secreting itself under various forms of cover, or occasionally burrowing in sand. Certainly neither geotropism nor stereotropism are equally or reasonably applicable as explanations of all these varied conditions and habits. I believe we are therefore forced to the conclusion that physiological conditions of adaptation are primarily involved, and that the various phases of behavior are so many expressions of such adjustments.

SYRACUSE UNIVERSITY,
January 1, 1907.

ON THE ANATOMY OF THE CENTRAL NERVOUS SYSTEM OF THE NINE-BANDED ARMADILLO (TATU NOVEMCINCTUM LINN.).[1]

LILY C. SHUDDEMAGEN.

The present paper is a contribution to the macroscopical anatomy of the brain, spinal cord, cranial and spinal nerves of the nine-banded armadillo.

There appears to be no literature on any portion of the central nervous system except the brain in any edentate, with the exception of Pouchet's classic account of *Myrmecophaga;* with this omission the relations of the spinal cord in this group are unknown, and the present description of that organ complex is an attempt to fill this hiatus in our knowledge. A list of the memoirs treating of the anatomy of the brain is appended at the end of the present paper; of those memoirs, the ones by Gervais (1869), Pouchet (1869), and notably Smith (1899) are the most important. Smith is the only writer who mentions the brain of the particular species examined by me, but gives no figures of it; and indeed, our knowledge of the general anatomy of this species is much more scant than of various other armadillos,— even the rare *Chlamydophorus*.

Comparisons of the brain of this species are made with the brains of other described Dasypodidæ, and I have followed Smith's nomenclature of the parts.

The material used consisted of four specimens, two males and two females, procured in the neighborhood of Austin, Travis County, Texas. Two of these were preserved in formalin and two in alcohol.

This work has been done entirely under the direction of Prof. Thos. H. Montgomery, Jr., and the writer is under great obligation to him for his helpful suggestions, and kindly sympathy and constant encouragement during the preparation of this memoir.

[1] Contributions from the Zoölogical Laboratory of the University of Texas, No. 75.

1. The Brain.

General Topography.

The brain is almost twice as long as broad. The bulbus olfactorius forms the most anterior, and the medulla oblongata its most posterior parts. The cerebrum broadens out posteriorly, and, on lateral view, is not quite as high as the cerebellum. The general shape is much like that of the lower mammals.

(*a*) *Prosencephalon.* — The prosencephalon is composed of the following parts: bulbus olfactorius, tuberculum olfactorium, lobus pyriformis, pedunculus olfactorius, locus perforatus, and the cerebral hemispheres.

The *bulbus olfactorius* (Pl. XXIV., Fig. 1, *Bul. Olf.*) is the most anterior part of the brain, and is relatively enormous. From a ventral view, it is seen to be heartshaped with the apex pointing forward. The ventral surface is indented by almost parallel furrows or sulci, running at right angles to the long axis of the brain. The dorsal surface (Fig. 4) is spherically rounded and smooth. It is placed somewhat ventral to the cerebral hemispheres (Fig. 2), so that over half of its dorsal surface is overlapped by them. From the anterior part of the bulbus olfactorius the olfactory nerve spreads out in a great fan-shaped mass.

The *tuberculum olfactorium* (Pl. XXIV., Fig. 1, *Tub. Olf.*) is a large oval area slightly raised above the surrounding regions. It is separated from the bulbus olfactorius by the pedunculus olfactorius. Its surface is not smooth, but somewhat tuberculated. It reaches a relatively large size in the armadillo.

The *lobus pyriformis* is visible along the lateral surface of the brain, just posterior to the tuberculum olfactorium; it consists of an anterior lobe (*Lob. Pyr. A.*, Fig. 2), and a posterior (*Lob. Pyr. P.*, Fig. 1).

The *pedunculus olfactorius* (Pl. XXIV., Fig. 3, *Ped. Olf.*) is to be seen only in a lateral view of the brain. It connects the bulbus olfactorius with the remainder of that organ. In both dorsal (Pl. XXIV., Fig. 4), and ventral (Fig. 1), views it is hidden by the cerebral hemispheres and the oblique position of the bulbus olfactorius.

The *locus perforatus* (Pl. XXIV., Fig. 1, *Loc. Perf.*) is the

depressed, quadrilateral area immediately anterior to the optic chiasma.

The *cerebral hemispheres* (Pl. XXIV., Figs. 2 and 4) show as high a development as any of the armadillos figured by Smith. The short *anterior rhinal fissure* (Pl. XXIV., Fig. 4, *Fis. Rh. A.*) begins in the boundary between the bulbus olfactorius and the hemispheres. It extends obliquely upwards for about a fourth of the length of the hemispheres. The *posterior rhinal fissure* (Pl. XXIV., Fig. 4, *Fis. Rh. P.*) begins near the posterior border of the hemispheres and runs horizontally towards the anterior part of the hemispheres, where it joins the sulcus β (Pl. XXIV., Fig. 4, β). In the most dorsal part of the hemispheres, the sulci γ and δ (Pl. XXIV., Fig. 4) are faintly developed. The latter of these two sulci corresponds to the suprasylvian sulcus of other mammals. On the mesial surface of the two hemispheres the sulcus limitans pallii (Pl. XXIV., Fig. 3, *Sul. L.*) is found.

In this animal, as in all mammals, a series of nerve fibers, or *commissures*, serve to connect homologous areas of the two hemispheres.

The most dorsally placed commissure is in the form of an inverted, obliquely placed U (Pl. XXIV., Fig. 3, *Cor. Cal.*). The arms of the U are formed by the corpus callosum (Pl. XXIV., Fig. 3, *Cor. Cal.*), and the ventral and dorsal psalterium (Pl. XXIV., Fig. 3, *Psal. V.* and *D.*). The curve of the U is formed by the splenium (Pl. XXIV., Fig. 3, *Spl.*). This commissure is placed more nearly vertical, and is rather smaller than in most of the edentate brains figured by Smith. There is really no apparent distinction between the dorsal and ventral psalterium. The psalterium is slightly longer than the corpus callosum. The two arms of this dorsal commissure are in contact with each other for the greater part of their extent, only the most ventral part of the psalterium extends a little further ventrally than the corpus callosum. The interval between the two arms of the dorsal commissure is called the septum lucidum in human anatomy. In the edentates, Smith calls this the paracommissural body. But since the two arms of the commissure are in contact with each other for the greater part of their extent, there is practically no septum lucidum or paracommissural body, in this armadillo.

The *anterior commissure* (Pl. XXIV., Fig. 3, *Com. A.*) is of fairly large size. It is a rather cylindrical bundle of fibers and connects the pyriform lobes. Because of the relatively large size of the pyriform lobes, the anterior commissure attains its increase of size. In the armadillos, all the parts of the brain connected with the sense of smell, reach relatively large dimensions.

(*b*) *Thalamencephalon.* — The thalamencephalon is the second embryological division of the brain, and consists of that part which bears the optic thalami, the infundibulum, pituitary body, and pineal body.

The *optic thalami* (Pl. XXV., Fig. 7, *Opt. Th.*) and the corpora quadrigemina (Pl. XXV., Fig. 7, *Cor. Q.*) form a large area of quadrilateral shape. The optic thalami are separated from each other, in the median line, by the third ventricle. They are connected across this ventricle by means of the commissura molli. This extends across the slit-like third ventricle as a large cylindrical mass of fibers (Pl. XXIV., Fig. 3, *Com. Mol.*). Thus the third ventricle becomes reduced to a narrow circular channel surrounding the commissura molli.

The floor of the third ventricle is drawn downward into a funnel-shaped pouch, the *infundibulum* (Pl. XXIV., Fig. 3, *Inf.*).

The *hypophysis* (Pl. XXIV., Fig. 3, *Hyp.*) is attached to the ventral part of the infundibulum.

The *pineal body* (Pl. XXV., Fig. 7, *Cor. Pin.*) lies in a shallow groove of the anterior corpora quadrigemina, just posterior to the third ventricle.

The *third ventricle* (Pl. XXV., Fig. 7, *Ven. III*) opens into the two first ventricles (Pl. XXV., Fig. 7, *Ven. I*) by means of the foramen of Monroe (Pl. XXV., Fig. 7, *For. M.*). Out of the posterior part of the third ventricle, the aqueduct of Sylvius (Pl. XXIV., Fig. 3, *Aq. Syl.*) opens and passes into the fourth ventricle.

The *II, or optic nerve* (Pl. XXIV., Fig. 1, *II*) comes off from the ventral surface of the brain, just a little anterior to the infundibulum. It is of very small size, because of the great diminution of the visual acuteness and consequent reduction of the size of the eye.

The *IV, or pathetic nerve* (Pl. XXIV., Fig. 1, *IV*) arises from

the ventral surface of the brain, just posterior to the infundibulum.

(*c*) *Mesencephalon.* — The mesencephalon is that embryological division of the brain which gives rise to the corpora quadrigemina and the crura cerebri.

The *corpora quadrigemina* (Pl. XXV., Fig. 7, *Cor. Q.*) lie immediately posterior to the optic thalami. The anterior pair of the corpora quadrigemina forms an area slightly elevated above the level of the optic thalami. Just posterior to them, the posterior pair of the corpora quadrigemina rise to a much higher level (Pl. XXIV., Fig. 3, *Cor. Q.*); their most dorsal point comes up almost to the level of the cerebral hemispheres. The corpora quadrigemina are wedged between the cerebellum and the cerebral hemispheres. In the armadillo, they are not separated across the middle, but form one body in which separation is only faintly indicated by a shallow longitudinal furrow. The reduction in the size of the anterior pair of the corpora quadrigemina is probably due to the waning importance of the sense of sight. The posterior corpora quadrigemina retain their large size, or perhaps even show an increase in size, because they are not connected as directly with the sense of sight.

The *crus cerebri* arises from under the optic tract as a faint, indistinct band of fibers, runs backwards and disappears under the pons Varolii.

(*d*) *Metencephalon.* — The embryological division of metencephalon gives rise, in the adult, to the cerebellum.

Viewed dorsally (Pl. XXIV., Fig. 4), the cerebellum presents a somewhat triangular shape, where the paraflocculi (Pl. XXIV., Fig. 4, *Par. Fl.*) and the posterior lobe (Pl. XXIV., Fig. 4, *Lob. P.*) form the three angles. The cerebellum is much convoluted, as is the case in all mammals. Its greatest diameter is transverse. This large cerebellar mass hides from view the entire fourth ventricle except the most posterior part (Pl. XXIV., Fig. 4, *Ven. IV*). The cerebellum is supported and connected with the brain stem by two cerebellar peduncles (Pl. XXV., Fig. 7, *Ped. Cer.*). Anteriorly, the cerebellum is closely adapted to the contour of the cerebral hemispheres. It projects forward sufficiently to hide the posterior corpora quadrigemina completely.

The most lateral projections of the cerebellum are two fairly large sized bodies. These bodies, composed of a number of folia and separated almost entirely from the remainder of the cerebellum by a fissure, are the *lobi flocculi.*

Each of these *lobi flocculi* consists of two distinct parts, the flocculus (Pl. XXIV., Figs. 1 and 2, *Floc.*) and the paraflocculus (Pl. XXIV., Figs. 2 and 4, *Par. Fl.*). The latter is much the largest of the two, and almost completely hides the former from view. From a dorsal view the paraflocculus (Pl. XXIV., Fig. 4, *Par. Fl.*) appears as a crescentic mass of folia, forming the lateral projections of the cerebellum.

Aside from the *lobi flocculi*, the remainder of the cerebellum may be divided into three lobes, the lobus anticus (Pl. XXIV., Fig. 4, *Lob. A.*), the lobus centralis (Pl. XXIV., Fig. 4, *Lob. C.*), and the lobus posticus (Pl. XXIV., Fig. 4, *Lob. P.*).

The *lobus anticus* (Pl. XXIV., Figs. 2, 3, and 4, *Lob. A.*) is separated from the posterior part of the cerebellum by the fissura prima (Pl. XXIV., Figs. 2, 3, and 4, *Fis. 1*). It is clearly visible in a dorsal view of the brain (Pl. XXIV., Fig. 4, *Lob. A.*), and is not hidden between the lobus centralis and the cerebral hemispheres, as is the case in the *Chlamydophorus* (Smith, 1899, Fig. 34) or in *Xenurus* (Smith).

The *lobus centralis* (Pl. XXIV., Figs. 2, 3 and 4, *Lob. C.*) is separated from the lobus posticus by means of the fissura secunda (Pl. XXIV., Figs. 2, 3 and 4, *Fis. 2*). It constitutes the largest and most complex part of the cerebellum. It is a large irregular area which has bulged forward and laterally, wedging its way between the lobus anticus and the lobus flocculus.

The *lobus posticus* (Pl. XXIV., Figs. 2, 3 and 4, *Lob. P.*) is the most caudal part of the cerebellum. It is small, consisting of but few folia, and covers over almost completely the posterior part of the fourth ventricle.

(*e*) *Myelencephalon.* — The embryonic division of myelencephalon gives rise, in tne adult, to the medulla oblongata and the pons Varolii.

The *medulla oblongata* (Pl. XXIV., Fig. 4, *Med. Obl.*) is the most posterior part of the brain, and is continued directly into the spinal cord. In the medulla oblongata is the fourth ventricle,

roofed over by a thin membrane. The greatest part of the medulla oblongata is covered over by the cerebellum.

The *pons Varolii* (Pl. XXIV., Fig. 3, *Pons*) forms the most anterior part of the hind brain. It is a pair of slight elevations on the ventral surface of the brain, a little posterior to the infundibulum.

From the medulla oblongata arise all the remainder of the cranial nerves, from the V to the XII inclusive.

The *V, or trigeminal nerve* (Pl. XXIV., Fig. 1, *V*) arises from the pons Varolii. It soon divides into two branches, the most lateral of which subdivides again.

The *VI, or abducent nerve* (Pl. XXIV., Fig. 1, *VI*) arises in the region of the pons Varolii, and runs to the external rectus eye muscle.

The *VII, or facial nerve* (Pl. XXIV., Fig. 1, *VII*) arises in close connection with the VIII nerve, in the region just laterad of the pons Varolii. It soon subdivides into branches.

The *VIII, or auditory nerve* (Pl. XXIV., Fig. 1, *VIII*) arises with the VII nerve from the same part of the brain. It runs directly outwards and enters the cochlea of the ear.

The *IX, or glosso-pharyngeal nerve* (Pl. XXIV., Fig. 1, *IX*) arises by several roots, from the ventral surface of the medulla.

The *X, or pneumogastric nerve* (Pl. XXIV., Fig. 1, *X*) arises by several roots from the medulla, just posterior to the IX nerve.

The *XI, or spinal accessory nerve* (Pl. XXIV., Fig. 1, *XI*) arises by several roots from the ventral surface of the medulla and the spinal cord. Some of its roots arise from the spinal cord, as far back as the fourth cervical nerve.

The *XII, or hypoglossal nerve* (Pl. XXIV., Fig. 1, *XII*) arises by several roots from the medulla oblongata, just posterior to the origin of the XI nerve.

2. Spinal Cord.

The spinal cord is cylindrical, but somewhat flattened dorso-ventrally. In the cervical and sacral regions, it has a slight enlargement from which the nerves of the brachial and lumbo-sacral plexuses are given off. In the sacral region the cord breaks up into a number of fine nerves which occupy the vertebral canal as the cauda equina. These nerve branches pass out,

pair by pair, from between the caudal vertebræ and supply the muscles of the tail.

The most anterior division of the spinal nerves is the cervical (Pl. XXVI., *C. 1–C. 8*). Of these there are eight pairs.

Of the thoracic nerves (Pl. XXVI., *T. 1–T. 10*) there are ten pairs.

The lumbar region is very short, containing six pairs of nerves (Pl. XXVI., *L. 1–L. 6*).

The sacral nerves (Pl. XXVI., *S. 1–S. 8*) are eight in number.

The exact number of the caudal nerves was not ascertained by me. But they are quite numerous, possibly as many as fifteen to twenty pairs.

(*a*) *Cervical Plexus.* — The cervical plexus (Pl. XXVI., *C. 1–C. 8*) is composed of the dorsal branches of the eight pairs of cervical nerves. These branches pass almost vertically upwards, interlace, and supply the dorsal neck muscles. On Pl. XXVI., on the right hand side of the drawing, are shown the dorsal branches of the cervical nerves.

(*b*) *Brachial Plexus.* — The brachial plexus is composed of the large ventral branches of the third, fourth, fifth, sixth, seventh, and eighth cervical nerves, and the first and second thoracic nerves. The formation of the plexus is due to the union of the several nerves, by means of strong connecting branches. The plexus lies in the axilla, and all the component nerves pass out laterally, almost parallel to the first rib. By means of its branches, the arm and shoulder are innervated.

The three *subscapular nerves*, the cranial (Pl. XXVI., *Sub. Sc. 1*), the middle (Pl. XXVI., *Sub. Sc. 2*), and the caudal (Pl. XXVI., *Sub. Sc. 3*), all supply muscles on the ventral surface of the scapula. The cranial subscapular nerve (Pl. XXVI., *Sub. Sc. 1*) arises from the third, fourth, and fifth cervical nerves. The middle subscapular nerve (Pl. XXVI., *Sub. Sc. 2*) arises from the sixth cervical nerve. The caudal subscapular nerve (Pl. XXVI., *Sub. Sc. 3*) arises from the sixth, seventh, and eighth cervical nerves.

The *suprascapular nerve* (Pl. XXVI., *Sup. Sc.*) arises from the fifth cervical nerve. It passes onto the dorsal side of the scapula and enervates the supraspinatus and infraspinatus muscles.

The *axillary nerve* (Pl. XXVI., *Ax.*) arises from the fifth and sixth cervical nerves. It supplies some muscles in the upper arm.

The *radiales nerve* (Pl. XXVI., *Rad.*) is one of the three nerves that supply the lower arm and hand. It arises from the sixth, seventh, and eighth cervical nerves.

The *medianus nerve* (Pl. XXVI., *Med.*) also principally supplies the muscles of the forearm and hand. It arises from the seventh, and eighth cervical, and the first thoracic nerves.

The *ulnaris nerve* (Pl. XXVI., *Uln.*) is the third lower arm and hand nerve. It arises from the eighth cervical, and first and second thoracic nerves.

(*c*) *Thoracic Plexus.*— From the first, second, and third thoracic nerves arise three ventral branches which pass out laterally and unite into a little separate plexus (Pl. XXVI., *X.*) Then this plexus gives off three main branches which subdivide again and again. All of these branches supply the great lateral skin muscle which is attached along the whole length of the armor. A plexus like this, to my knowledge, is not present in any other mammal. It has probably arisen because of the great development of the large skin muscle, which attaches to the sides of the armor and functions in drawing the animal together in a ball. Because of its origin from the thoracic nerves, I have taken the liberty of naming it the thoracic plexus.

The remainder of the thoracic nerves are arranged similarly to those of other mammals. They divide into two branches almost immediately after leaving the intervertebral foramina. The dorsal branches supply the superficial muscles of the back, while the ventral branches run along the ribs as the intercostal nerves.

(*d*) *Lumbar Nerves.* — The first three lumbar nerves take no part in the formation of the lumbo-sacral plexus. The ventral branch of the first lumbar nerve divides into two branches, the ilio-hypogastric (Pl. XXVI., *Il. Hyp.*), and the ilio-inguinal (Pl. XXVI., *Il. Ing.*). The ventral branch of the second lumbar nerve forms the genito-crural nerve (Pl. XXVI., *Gen. Cr.*). The third lumbar nerve forms the external cutaneous nerve (Pl. XXVI., *Ext. Cut.*).

(*e*) *Lumbo-Sacral Plexus.* — The lumbo-sacral plexus is com-

posed of the fourth, fifth, and sixth lumbar, and the eight sacral nerves. These nerves are all interconnected by strong branches, and they supply the muscles of the thigh and lower limb.

The *anterior crural nerve* (Pl. XXVI., *Ant. Cr.*) is composed of parts of the fourth, fifth, and sixth lumbar nerves. It supplies some of the upper thigh muscles.

The *obturator nerve* (Pl. XXVI., *Obt.*) arises from the sixth lumbar and first sacral nerves. It also goes to supply some of the upper thigh muscles.

The *sciatic major nerve* (Pl. XXVI., *Sc. Maj.*) arises from the sixth lumbar, and first, second, and third sacral nerves. This is the great nerve of the posterior limb. It soon divides into the tibialis (Pl. XXVI., *Tib.*), the perroneus (Pl. XXVI., *Per.*), the gluteous (Pl. XXVI., *Glut.*), and the sciatic minor nerve (Pl. XXVI., *Sc. Min.*).

The *pudendus nerve* (Pl. XXVI., *Pud.*) arises from the fourth sacral nerve.

The *cutaneous femoris nerve* (Pl. XXVI., *Cut.*) arises from the fifth sacral nerve.

General Remarks.

The brain has been previously described for the following Dasypodids :

The brain of *Chlamydophorus truncatus* has been figured and described by Smith (1899) and Pouchet (1869). Hyrtl (1855) gives just a few brief notes on the brain, without any figures.

Dasypus sexcinctus has been figured and described by Smith (1899), Turner (1867), and Pouchet (1869).

Priodon gigas has been figured by Pouchet (1868 and 1869), and mentioned by Smith (1899).

Tolypeutes tricinctus has been mentioned by Smith (1899), and figured and described by Gervais (1869).

Tatu novemcinctum has been mentioned by Smith (1899), without figures.

Tatu peba has been figured and described by Smith (1899) and Rapp (1852).

Xenurus unicinctus has been figured and mentioned by Smith (1899) and Garrod (1878).

Dasypus villosus has been figured and described by Smith (1899).

Smith's (1899) work on the Armadillos is by far the most important, and for this reason I have compared the species under present consideration with his descriptions.

The brain of *Tatu novemcinctum* shows less similarity with the genus *Chlamydophorus*, than with the brain of any other genus of armadillo. To judge by the figure of *Xenurus unicinctus* given by Garrod (1878), there seems to be greater similarity of the brain of *Tatu* with *Xenurus* than with any other genus of armadillo. The fissures, sulci, and the general shape and contour of these two brains have very many points in common. However, much more detailed study must be made of all the species of *Armadillo* before one could venture to assert this with any degree of certainty.

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DESCRIPTION OF THE PLATES.

The following abbreviations have been used:

(Greek letters denote sulci.)

Ant. Cr.	anterior crural.
Aq. Syl.	aqueductus Sylvii.
Ax.	axillary.
Bul. Olf.	bulbus olfactorius.
C. 1–8.	cervical nerves.
Com. A.	commissura anterior.
Com. Mol.	commissura mollis.
Com. P.	commissura posterior.
Cor. Cal.	corpus callosum.
Cor. Pin.	corpus pineale.
Cor. Q.	corpora quadrigemina.
Cut. Fem.	cutaneus femoris posterior.
Ex. Cut.	external cutaneous.
Fis. 1.	fissura prima.
Fis. 2.	fissura secunda.

Fis. Rh. A.	anterior rhinal fissure.
Fis. Rh. P.	posterior rhinal fissure.
Floc.	flocculus.
For. M.	foramen of Monro.
Gen. Cr.	genito-crural.
Glut.	glutæus inferior.
Hipp.	hippocampus.
Hyp.	hypophysis.
Il. Hyp.	ilio-hypogastric.
Il. Ing.	ilio-inguinal.
Inf.	infundibulum.
L. 1–10.	lumbar nerves.
Lob. A.	lobus anticus.
Lob. C.	lobus centralis.
Lob. P.	lobus posticus.
Lob. Pyr. A.	lobus pyriformis anterior.
Lob. Pyr. P.	lobus pyriformis posterior.
Loc. Perf.	locus perforatus.
Med.	medianus.
Med. Obl.	medulla oblongata.
Obt.	obturator.
Opt. Th.	optic thalami.
Par. Fl.	paraflocculus.
Ped. Cer.	pedunculi cerebelli.
Ped. Olf.	pedunculus olfactorius.
Per.	peroneus.
Psal. D.	psalterium dorsale.
Psal. V.	psalterium ventrale.
Pud.	pudendus.
Rad.	radialis.
S. 1–8.	sacral nerves.
Sc. Maj.	major sciatic.
Sc. Min.	minor sciatic.
Spl.	splenium.
Sub. Sc. 1.	cranial subscapularis.
Sub. Sc. 2.	middle subscapularis.
Sub. Sc. 3.	caudal subscapularis.
Sul. L.	sulcus limitans pallii.
Sup. Sc.	suprascapularis.
T. 1–10.	thoracic nerves.
Tib.	tibialis.
Tr. Opt.	tractus opticus.
Tub. Ac. L.	tuberculum acusticum laterale.
Tub. Ac. M.	tuberculum acusticum median.
Tub. Olf.	tuberculum olfactorium.
Uln.	ulnaris.
Ven. I.–IV.	ventricles I.–IV.
I.–XII.	cranial nerves.

Explanation of Plates.

All the figures are from enlarged freehand sketches. The figures on Plates I. and II. were drawn twice natural size, and then reduced about one third in the reproduction. Plate III. was drawn natural size, and then reduced about one half in the reproduction.

Plate XXIV.

Fig. 1. Ventral view of the brain.
Fig. 2. Lateral view.
Fig. 3. Median longitudinal section.
Fig. 4. Dorsal view.
Fig. 5. Ventral view of a late fœtal brain; length of the fœtus was about 15 cm.
Fig. 6. Dorsal view of the same late fœtal brain as Fig. 5.

Fig. 1

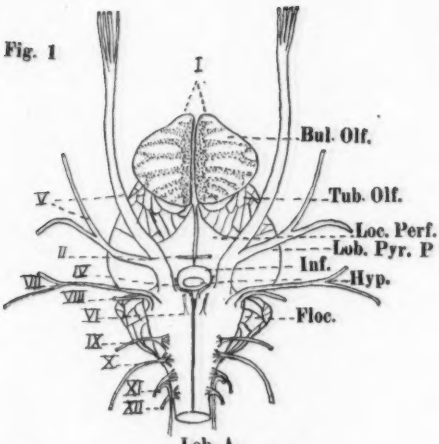


Fig. 6

Fig. 5

Fig. 2

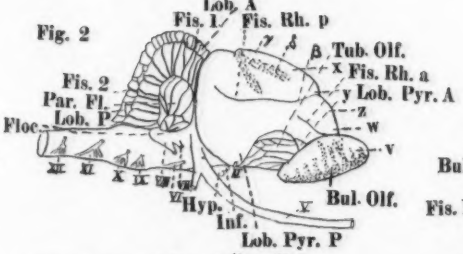


Fig. 4

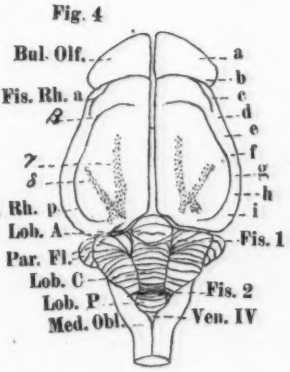


Fig. 3

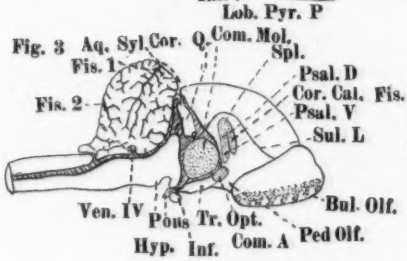


PLATE XXV.

FIGS. 7–11. Horizontal, longitudinal sections of the brain. The dotted parts of the figures show the ventricles.

FIG. 7. The dorsal surface of a horizontal section; taken in plane *v* of Fig. 2.

FIG. 8. The dorsal surface of a horizontal section, taken in the plane *w* of Fig. 2.

FIG. 9. The dorsal surface of a horizontal section, taken in the plane *z* of Fig. 2.

FIG. 10. The dorsal surface of a horizontal section, taken in the plane *y* of Fig. 2.

FIG. 11. The dorsal surface of a horizontal section, taken in plane *x* of Fig. 2.

FIGS. 12–20 are cross-sections of the brain, beginning at the anterior end.

FIG. 12. The caudal surface of a cross-section taken in the plane *a* of Fig. 4.

FIG. 13. The caudal surface of a cross-section taken in the plane *b* of Fig. 4.

FIG. 14. The caudal surface of a cross-section taken in the plane *c* of Fig. 4.

FIG. 15. The caudal surface of a cross-section taken in the plane *d* of Fig. 4.

FIG. 16. The caudal surface of a cross-section taken in the plane *e* of Fig. 4.

FIG. 17. The caudal surface of a cross-section taken in the plane *f* of Fig. 4.

FIG. 18. The caudal surface of a cross-section taken in the plane *g* of Fig. 4.

FIG. 19. The caudal surface of a cross-section taken in the plane *h* of Fig. 4.

FIG. 20. The caudal surface of a cross-section taken in the plane *i* of Fig. 4.

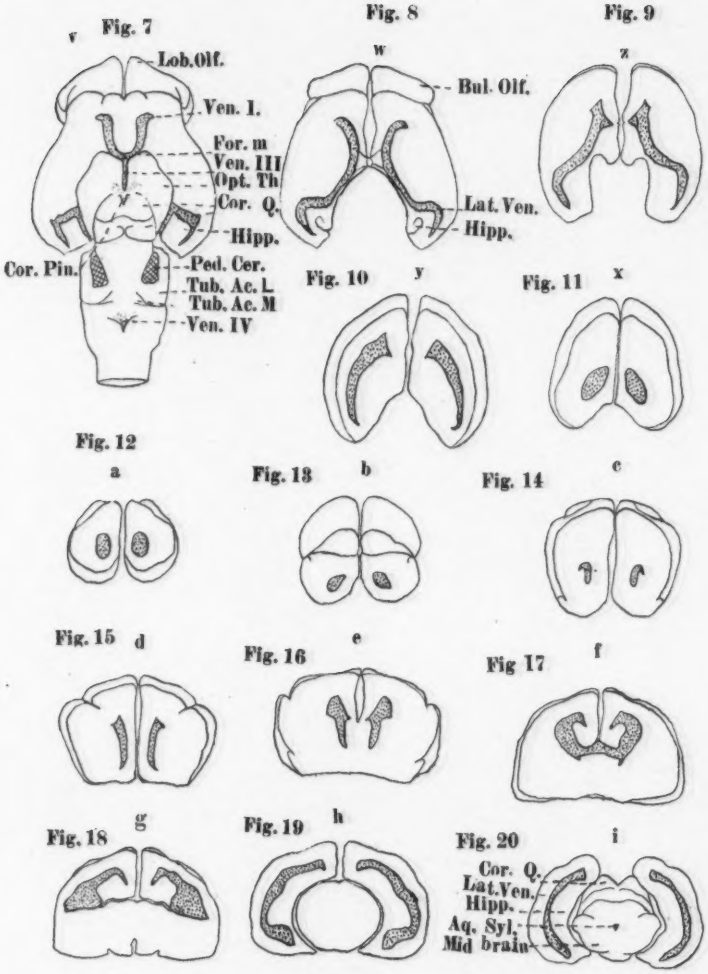
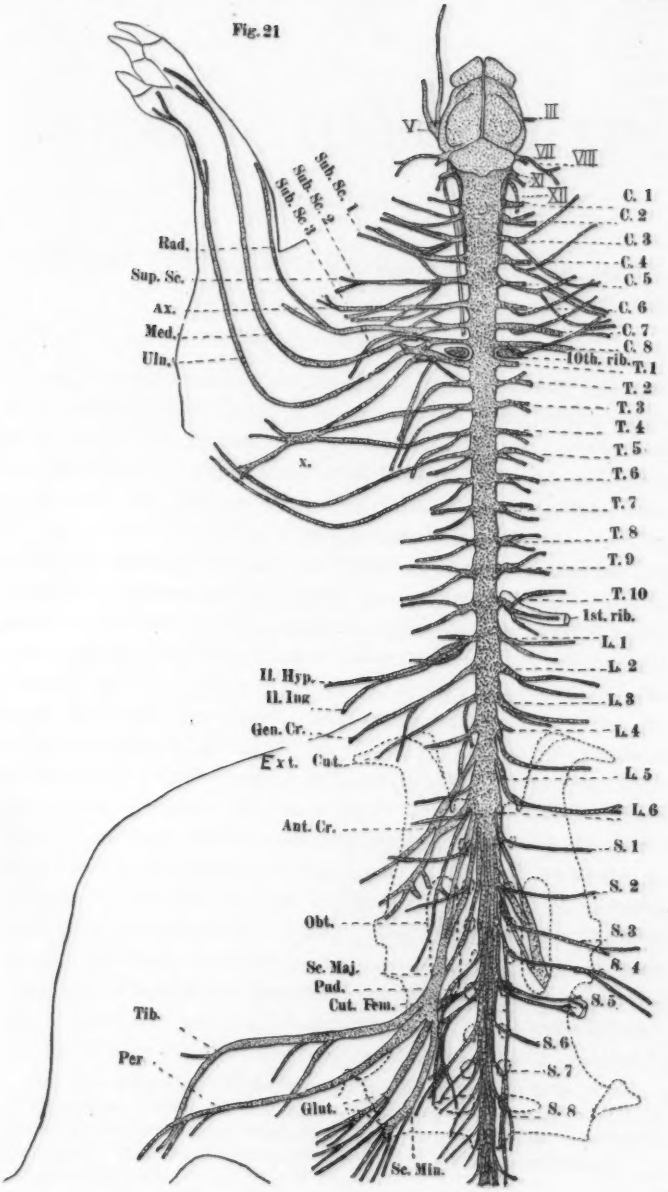

v
Fig. 7
Lob.Olf.
Ven. I.
For. m
Ven. III
Opt. Th
Cor. Q.
Hipp.
Cor. Pin.
Ped. Cer.
Tub. Ac. L
Tub. Ac. M
Ven. IV
w
Fig. 8
Bul. Olf.
Lat. Ven.
Hipp.
z
Fig. 9
y
Fig. 10
x
Fig. 11
Fig. 12
a
Fig. 13
b
Fig. 14
c
Fig. 15
d
Fig. 16
e
Fig 17
f
Fig. 18
g
Fig. 19
h
Fig. 20
i
Cor. Q.
Lat.Ven.
Hipp.
Aq. Syl.
Mid brain

PLATE XXVI.

FIG. 21. A drawing of the entire central nervous system. The dotted lines show the outline of the sacrum in its natural relation to the spinal nerves. The nerves on the left hand side of the figure are all the ventral branches of the spinal nerves. On the right hand side of the figure, the more superficial branches of the spinal nerves are shown.

Fig. 21


V.
III
VII
VIII
XI
XII
Sub. Sc. 1.
Sub. Sc. 2.
Sub. Sc. 3.
Rad.
Sup. Sc.
Ax.
Med.
Uln.
X.
C. 1
C. 2
C. 3
C. 4
C. 5
C. 6
C. 7
C. 8
10th. rib.
T. 1
T. 2
T. 3
T. 4
T. 5
T. 6
T. 7
T. 8
T. 9
T. 10
1st. rib.
L. 1
L. 2
L. 3
L. 4
L. 5
L. 6
S. 1
S. 2
S. 3
S. 4
S. 5
S. 6
S. 7
S. 8
Il. Hyp.
Il. Ing.
Gen. Cr.
Ext. Cut.
Ant. Cr.
Obt.
Sc. Maj.
Pud.
Cut. Fem.
Tib.
Per.
Glut.
Sc. Min.